CONTRIBUIÇÃO PARA O CONHECIMENTO DA FAUNA DO KIMERIDGIANO DA MINA DE LIGNITO GUIMAROTA (LEIRIA, PORTUGAL)

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LISBOA
1973

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LIZARDS FROM CENTRAL PORTUGAL

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JUERGEN SEIFFERT

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PREFACE

«The evolutionary story of the Lacertilia is divided into two very unequal portions, a Triassic--Jurassic chapter very poorly known, and a fairly well-documented story beginning in the late Cretaceous and extending to the present; between the two there is an intermezzo formed by the appearance of the mosasaurs and other aquatic lizards of the Cretaceous.»

(ALFRED SHERWOOD ROMER, 1968)

«As to how long the Kuehneosaurs (or the eolacertilians) persisted we can only conjecture. The eolacertilians possible were caught up in the wave of reptilian extinction that marked the close of the Triassic; if so, they must given rise to the later lizards before then. Conversely, they may have continued into the early Jurassic, when they became the ancestors of some of the lizards that appear as well-established forms in the late Jurassic.»

(EDWIN HARRIS COLBERT, 1970)

Within the actual knowledge of lacertilians and their evolution the occurrence of Triassic and Jurassic lizards leads to a conclusive importance. In the Upper Triassic the lacertilian morphogenesis was already completed and indeed to a highly specialized degree which is documented by the appearance of gliding forms (see ROBINSON, 1962; COLBERT, 1970). On the other hand the hitherto known Jurassic references are specimens of an insufficient evidence, excepting the numerous Lower Kimmeridgian remains from the Portuguese coalmine, Guimarota (see KÜHNE, 1968). Such forms are also found in the Upper Kimmeridgian sediments on shore about 70 km SW of the locality Guimarota. The Upper Jurassic lizards of Portugal presented here enlarge the record of the lacertilian evolution.

W. G. KÜHNE has explored mesozoic tetrapods for more than 30 years and hereby discovered the important localities of fossil vertebrates from the Rhaetian of England and the Kimmeridgian of Portugal. In my studies of the Portuguese skeletal remains Prof. KÜHNE encouraged me with critical advice. I am grateful to him and his former staff, particularly to Prof. B. KREBS and Miss E. DRESCHER for the assistance to my work carried out at the Institute of Paleontology, Free University Berlin.

The evidence of the rich vertebrate material from Portugal would not have been revealed without Prof. S. HENKEL's mission in the field. For the photographs produced with the scanning electron microscope, I am indebted to Prof. J. G. HELMCKE of the Max-Planck-Institute of Micromorphology and his team in the Technical University Berlin. I would especially like to thank Dr. PAMELA L. ROBINSON, London for the kind gift of a comparison material *(Kuehneosaurus)* from an Upper Triassic fissure-filling at Emborough, England. Finally I would like to express my thanks to Mr. P. BERNDT and Miss M. GRADE for drawing most illustrations in the text.

Deserving thanks, the Deutsche Forschungsgemeinschaft has generously subsidized the Guimarota researching project.

The present contribution is, in the main, a translation of my thesis on the Upper Jurassic Lacertilia from the Guimarota mine, added to which are the lacertilian remains of the Upper Kimmeridgian from Porto das Barcas and Porto Pinheiro.

A. Introduction

South of the Central Portuguese provincial town of Leiria lies the coalmine Guimarota. There lignite was mined, but utilized only for the lime-kiln in the vicinity of the mine and 10 years ago the output ceased. Recently, in 1972, Guimarota was reopened by Prof. HENKEL's enterprise with the expectation of discovering the complete skeletons of Jurassic mammals.

Until now, more than a thousand lacertilian fragments of the numerous vertebrate remains have been obtained from the layer FA$_{11}$ of the geological section exposed in the pit (see HELMDACH, 1968). Of these, the smaller part was yielded by manual splitting of the coal, the main part by washing and dressing the pit heap (for the methods see HENKEL, 1966, KÜHNE, 1968).

The stratigraphic position of the Guimarota complex has been determined by the ostracods as Lower Kimmeridgian (see HELMDACH, 1971). There appear *Cetacella inermis* MARTIN, 1958, *Dicrorygma kimmeridgensis* KILENYI, 1969, *Poisia bicostata* and *P. clivosa* HELMDACH, 1968, *Theriosynoecum hemigymnon* HELMDACH, 1968 and *Th. wyomingense* (BRANSON, 1935), *Timiriasevia mackerrowi* BATE, 1965. Their vertical distribution is shown in Fig. 1.

Apart from the Guimarota, two additional localities with tetrapod remains had already been discovered in 1961 on the Mid-Portuguese coast. Methodical exploitations of the most promising beds were undertaken at Porto das Barcas (Monti) and Porto Pinheiro in 1962, 1967 and 1968. The tow places are not more than 3 km apart. The stratigraphic age of the layers was determined by the appearance of the ostracod *Cetacella armata* MARTIN, 1958 as Upper Kimmeridgian (see KRUSAT, 1969, HELMDACH, 1971). The lacertilian fragments from the two Upper Kimmeridgian localities can be included among distinct taxa of the Guimarota-Lacertilia.

The vertebrate faunae, which the Upper Jurassic sediments of Portugal yielded until now, will be morphologically described in separate taxonomic groups by several contributors of the Institute of Paleontology, Free University Berlin.

The subject of the study presented here is the lacertilian material obtained from the Guimarota pit and the coastal localities Porto das Barcas and Porto Pinheiro.

The term «lacertilian» is to be used for Lacertilia (= Sauria) *sensu lato,* i. e. the group Lacertilia comprising the pro- and eolacertiformes. In the systematic classification the lizards were first named «Sauria» «McCARTNEY, 1802, but now the term «Lacertilia» WAGLER, 1830 in the meaning after GÜNTHER, 1867 has been accepted. In the zoological system the lacertilians are placed as following:

Class — Reptilia
Subclass   Lepidosauria
Order$_1$ Araeoscelidia
Order$_2$ Eosuchia
Order$_3$ Squamata (Lecertilia *s. l.* and Ophidia)
Order$_4$ Rhynchocephalia.

The known abundance of lacertilian forms is distributed in the taxonomic categories mentioned below (following the system after ROMER, 1966):

Lacertilia (= Sauria) sensu lato

1.   Infraorder. — *Prolacertiformes*
        Prolacertidae
        Thalattosauridae
        Tanystropheidae

2. Infraorder. — *Eolacertilia*

    Kuehneosauridae
    Cteniogenyidae SEIFFERT, 1970

3. Infraorder. — *Gekkota* (= Nyctisauria)

    Gekkonidae
    Pygopodidae

4. Infraorder. — *Iguania*

    ?Teilhardosauridae
    Agamidae
    Iguanidae
    Chamaeleonidae

5. Infraorder. — *Scincomorpha* (= Leptoglossa)

    ?Ardeosauridae
    Xantusiidae
    Scincidae
    Cordylidae (incl. Gerrhosauridae, Zonuridae)
    Lacertidae
    Teiidae
    ?Dibamidae

6. Infraorder. — *Anguimorpha* (= Diploglossa)

Superfamily$_1$: Anguoidea

    Anguidae
    Anniellidae
    Xenosauridae (incl. Shinisauridae)

Superfamily$_2$: Varanoidea (Platynota)

    Varanoidea (Platynota)
    Dorsetisauridae HOFFSTETTER, 1967
    Aigialosauridae
    Mosasauridae
    Dolichosauridae
    ?Necrosauridae
    Parasaniwidae
    Helodermatidae
    Varanidae
    Lanthanotidae
    Palaeophidae (Cholophidae)
    Simoliophidae

7. Infraorder. — *Amphisbaenia* (= Annulata)
    Amphisbaenidae.

idea of evolution results to account for the the paleontological documents, the following From the comparative morphology of origin and the phylogeny of lacertilians:

SCINCOMORPHA   ANGUIMORPHA   AMPHISBAENIA   Ophidia

GEKKOTA   IGUANIA   SCINCO – ANGUIMORPHA

EOLACERTILIA

Lacertilia s.l. – PROLACERTIFORMES   Rhynchocephalia

Eosuchia

Araeoscelidia

Captorhinomorpha

Prae – Microsauria

The standard profile section of the Guimarota mine and the more distant environs (Fig. 1):

The preceding Lusitanian section has been composed of corresponding statements (from HELMDACH, 1966, 1968, HÖLDER, 1964, MOUTERDE et al., 1971, LAPPARENT & ZBYSZEWSKI, 1957, RUGET-PERROT, 1961 and ZBYSZEWSKI, 1965).

As the underlying bed of the 2. Lusitanian lignite series, a rich shelly layer with *Isognomon* and *Trigonia* is supposed to mark the stratigraphic division of Upper Oxfordian and Lower Kimmeridgian. The marls with driftwood of Porto das Barcas and Porto Pinheiro are stratigraphycally ranged by the appearance of the ostracod *Cetacella armata* MARTIN, 1958 (see HELMDACH, 1971) and also by the evolutionary degree of the Mesozoic mammals compared with the findings of the Guimarota.

The special facies profile of the Guimarota is quoted from HELMDACH's thesis (1968). The specifications of the ostracods relate to their first appearance in the section. The vertical hachure signifies partly carboniferous layers. In the general map (after RUGET-PERROT, 1961) the vertical hachure marks the distribution of the Middle Portuguese Mesozoic surrounded with crystalline rocks and the Paleozoic.

The coalmine Guimarota is situated about 1,5 km SSE of the midtown, Leiria. The approach to the mine branches off from the main road Leiria-Cortes, opposite the branch to Vidigal (see HELMDACH, 1966). The geographical co-ordinates of the locality are after the Carta Militar de Portugal (sheet Leiria, No. 297) 142,75 NS (resp. 0°20')/307,5 EW or the degree of longitude 8°48'/of latitude 39°43'.

The Upper Jurassic vertebrate fauna of the Guimarota mine is composed in unequal amounts of representatives of the following systematic groups:

Osteichthyes	Holostei
	Teleostei (Otolithi)
Chondrichthyes	Selachii
Lissamphibia	Urodela
	Anura
Chelonia	Cryptodira
Lepidosauria	Eosuchia
	Lacertilia s. l.

Standard profile of the Guimarota mine
and the more distant environs :

Fig. 1 — Standard profile of the Guimarota mine and the more distant environs.
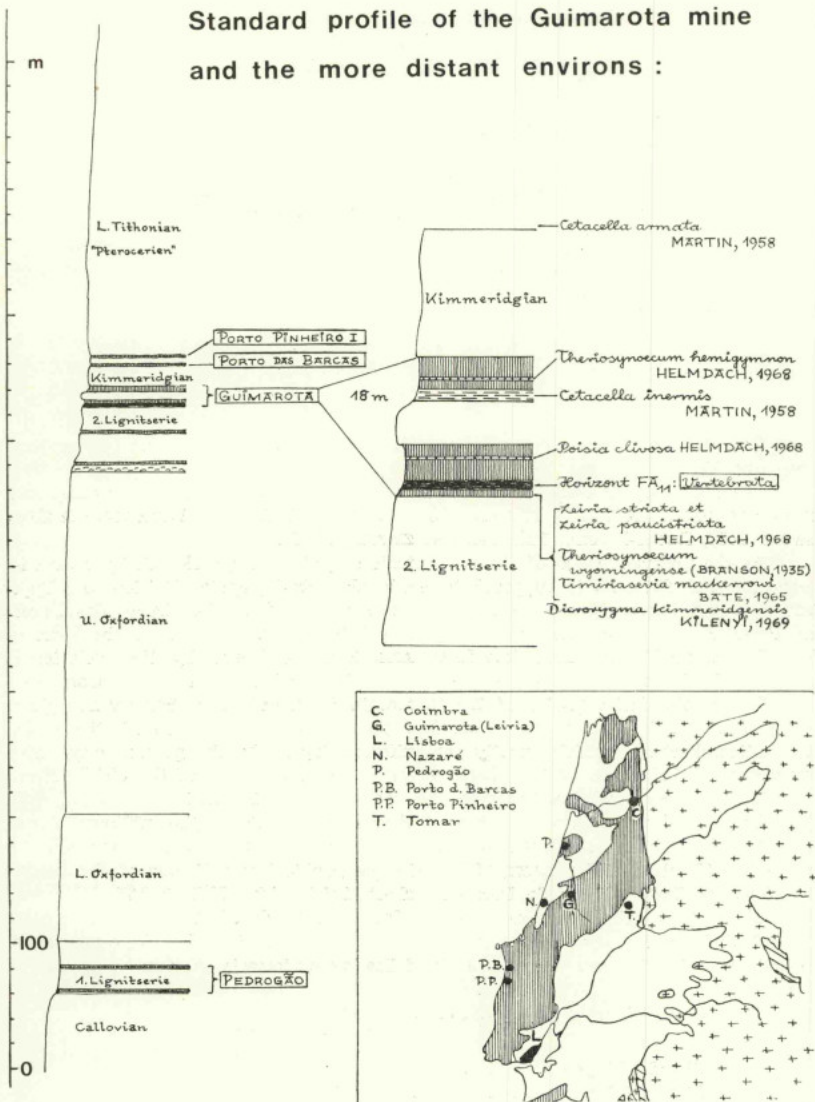
Archosauria . . . . Crocodilia
                            Pterosauria
                            Saurischia
                            Ornithischia

Mammalia . . . . Docodonta
                            Multituberculata
                            Pantotheria.

B. *Cteniogenys reedi* SEIFFERT, 1970

   Kuehneosaurus ROBINSON, 1962 and *Kuehneosuchus* ROBINSON, 1967a, both from the
Upper Keuper of England, and *Icarosaurus* COLBERT, 1966 from the Upper Triassic of
North-America are ancestral lacertilian types being not unspecialized on all accounts.
The vertebral column and the ribs of these forms are developed for gliding similarly
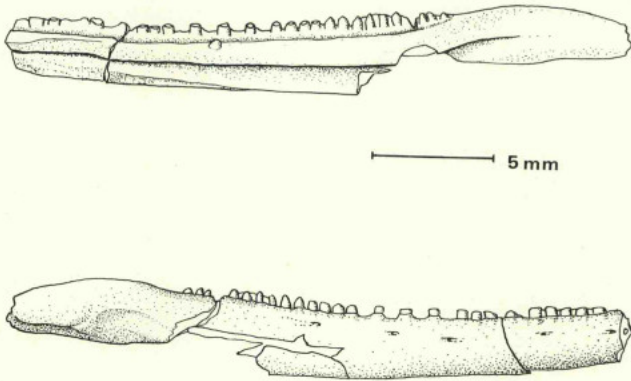

├──────────────┤ 5 mm

Fig. 2 — Gui. 51, right dentary of *Cteniogenys reedi;* notice the replacement
tooth on the lingual side and the attachment area for the angular on the
posterior part of the external side (below).

those of the recent gliding lizard *Draco* (Agamidae). Our knowledge about the Mesozoic
small reptiles is relatively scant by the fact that most of the known Jurassic and Cre-
taceous sediments are marine formations. In regard to the high degree of specialization
of the Upper Triassic gliding lizards we can expect, that additional lacertilian fin-
dings will reveal the variety of the early specializations. This postulate of ROMER
(1966) is verified with the presence of the Upper Jurassic Lacertilia from Portugal.
   From the «mammal layer» of the Upper Jurassic Morrison-Formation in «Quarry
No. 9» Como Bluff, Albany County, Wyoming ten specimens of a lacertilian incertae
sedis have become known. At first in 1909 GILMORE has published a broken dentary
(U. S. National Museum, Catalogue No. 6134), describing this one as holotype of *Cte-
niogenys antiquus* in 1928. The other nine remains, already found by W. H. REED in
1879, 1881, 1882 and preserved in the Yale Museum, were just identified as *Cteniogeys*
by GILMORE (1928).

In the coalmine Guimarota the same genus, but an other species is recovered with a lot of fragmentary jaw-bones. The Guimarota species also appears in the fauna of the two Upper Kimmeridgian localities Porto das Barcas and Porto Pinheiro.

Family Cteniogenyidae SEIFFERT, 1970

Type genus: *Cteniogenys* GILMORE, 1828.

Diagnosis. — (see GILMORE, 1928, p. 162-164, pl. 20).
Very long and slender dentaries with more than 35 teeth disclosed as cylindric-conical with slightly compressed crowns, pleuro-thecodont and hollow. The convex external surface is grooved by foramina in a line running parallel to the dentary border (crista dentalis). The Meckelian groove is exposed at the lingual side of the dentary.
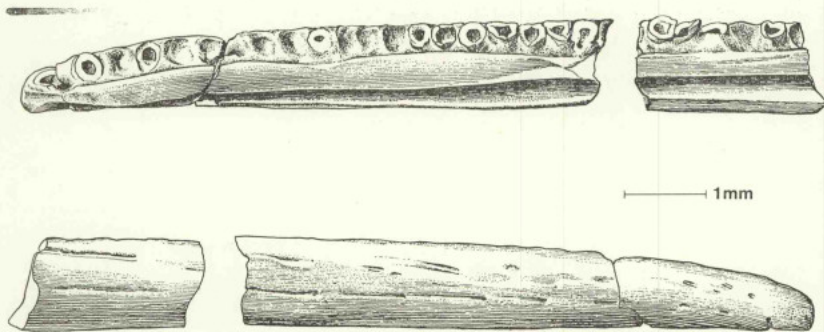

├──────────────┤ 1mm

Fig. 3 — Gui. A. 33, *Cteniogenys reedi*, right dentary (holotype); above: lingual view showing the extended subdental ridge and the Meckelian groove; below: labial view, remarkable groovings and foramina.

Type species of the genus. — *Cteniogenys antiquus* GILMORE, 1928 (No. 6134 of the U. S. Nat. Mus., coll. MARSH-party besides a nominated paratype No. 1068 and eight further specimens in the Yale Museum, coll. REED). In 1909 the dentary fragment of the holotype was delivered with 25 teeth, but because of the fragility of the specimen 24 teeth were still preserved in 1928.

Derivatio nominis of the new species from Portugal. — *reedi:* after W. H. REED, whose collection of nine specimens from Wyoming has helped to clear up the form *Cteniogenys.*

Holotype. — A right dentary, Gui. A. 33.

Formation and locality. — In the Kimmeridgian of Portugal.

Diagnosis and description of the species. — Extended jaws with ca. 40 conical teeth and more, showing characteristic peated enamel (striae) on the lingual side of the superior part of the teeth. As those of *Kuehneosaurus* ROBINSON, 1962 from the Upper Keuper of Emborough Quarry, England (s. dentary P. L. R. 53 of ROBINSON's collection) there are mostly to be seen about seven striae, of which the both external ones converge subparallelly with the outline to lingual cutting edges on the cusp (Pl. 1, 3). This feature is certainly affected by function of the masticators and by the food. The

dentary has in common the presence of a very low parapet of bone along the labial side of the teeth, and to which the teeth adhere close to their bases on their labial sides. The mode of tooth implantation is non-thecodont, rather subpleurodont; the teeth are fastened by attachment bone around their bases. The tooth replacement occurs by resorption close to, but not at the hollowed base of the old tooth, and the new tooth arises lingually to the old one. The dentaries have an elongated subdental ridge and a slender, lingually running Meckelian groove, anteriorly forming a ventral fossa at the symphyseal area. The symphysis of *Cteniogenys* is slight and obviously car-
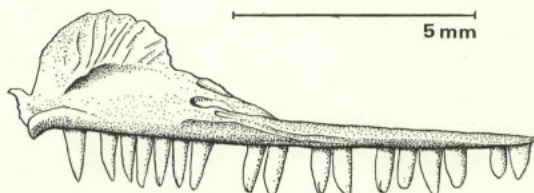

Fig. 4 — Gui. L. 234, right maxilla of *Cteniogenys reedi*, lingual view.

tilaginous-ligamentous. The Meckelian groove is extensively covered with the splenial indicated by the attachment area on the lingual surface of the subdental ridge. The posteriorly broad splenial thins in the middle of the dentary up to the symphysis. A separate canalis alveolaris inferior opens approximately under the 26th-30 th tooth (about under the fifteenth from behind). Ahead of this foramen the attachment area of the splenial distinctly continues on the anterior subdental ridge. Equally the attach-
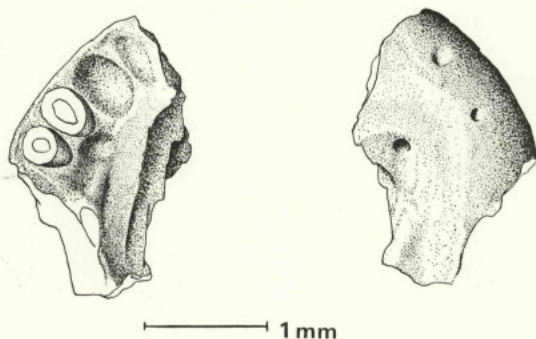

Fig. 5 — Gui. 345, right premaxilla of *Cteniogenys reedi*.

ment of the angular stretches to the anterior part of the dentary, running on the inferior border. The attachment areas are well to be seen on the specimens Gui. 51, Gui. A. 21, Gui. A. 26 like on *Kuehneosaurus* (cf. material of P. L. ROBINSON, London). From the appearance of the specimen Gui. 51 *Cteniogenys reedi* seems to lack a sepa-rate coronoid as *Kuehneosaurus*. «This element may have been present as a small bone» (COLBERT, 1970 about *Icarosaurus* and *Kuehneosaurus*). The posterior part of the jaw

cannot be diminished, because the insertion of the M. adductor mandibularis takes place in an areal dimension (cf. contrary to *Ophryoessa superciliosa,* a long-snouted iguanid).

The long stretched maxilla reveals a large and anterior advanced orbit. Thus the facial skull gives the impression of being relatively short. The maxillae rise dorsally only with the anterior part of the bone (s. Gui. 286, Gui. 332, Gui. L. 234).
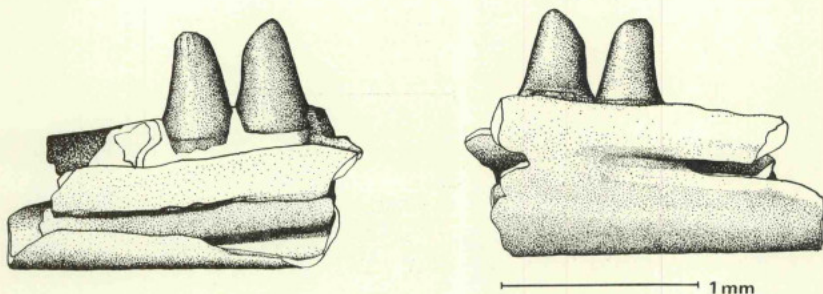

Fig. 6 — Fragment of a right dentary of *Cteniogenys reedi* (Porto Pinheiro I. L. 27), left: lingual view; right: labial view.

On their internal side there exist two foramina probably for the passage of nerve fibres of the N. V$_2$ with a parasympathetic portion of the N. VII (after HALLER v. HALLERSTEIN, 1934 there are very close connexions between the trigeminus and the facialis). As to be seen of the recent *Tupinambis* those rami (N. vidianus) of the N. pterygo-palatinus pass through an opening formed by the palatine as basal, the maxilla as lateral and the lacrimal as dorsal bordering; they unite the N. infraorbitalis (rr. maxillares alveolares,
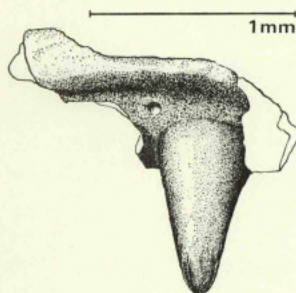

Fig. 7 — Maxillary tooth of *Cteniogenys reedi* (Porto das Barcas 1962).
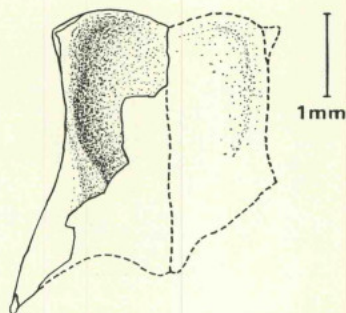
Fig. 8 — Gui. 82, parietal probably of *Cteniogenys reedi.*

rr. cutanei externi et rr. salivares) with rami communicantes aborales. For the nerval exit there are located foramina maxillo-facialia on the external side of the maxilla. As particularity the internal side of the right maxilla Gui. L. 234 anteriorly has a concavity and above it a fine lamellar longitudinal fanning caused by the affixture of the nasal. The nares of *Cteniogenys reedi* are apparently proceeded between the premaxillae to the mesial line (s. Gui. 345); the naris is obviously unpaired as that of *Kuehneosaurus.*

Paired parietal bones in the Guimarota material might add to *Cteniogenys reedi* (s. Gui. 82, Fig. 8) on account of the adequate presence of *Kuehneosaurus* and *Icarosaurus*.

Discussion. — There is an extensive conformity with the dentaries and maxillae of *Kuehneosaurus* ROBINSON, 1962 and *Icarosaurus* COLBERT, 1966 and those of *Cteniogenys reedi*. As distinguished from *Cteniogenys* the subdental ridge of *Kuehneosaurus* becomes more thin anteriorly and rather conssiderably on the posterior part of the dentary; apparently this causes the surangular to extend further in the forepart. On the nominated paratype *Cteniogenys antiquus* GILMORE, 1928 reveals a rule-shaped subdental ridge of a certain, constant height contrary to *Kuehneosaurus* and *Cteniogenys reedi*.

The Lusitanian *Cteniogenys reedi* corresponds essentially with the morphology of the jaws, to the Upper Triassic gliding lizards. The anatomy of the pleurothecodont teeth is identical as is the number (ca. 40 and more). The length of the jaws, the straight Meckelian groove in the dentary, the uniformity and the mode of tooth attachment, the slight symphysis and the skull bones in pairs refer to the eolacertilian nature of *Cteniogenys*. Dr. ROBINSON supposes the Upper Triassic gliding lizards to be a separate family (Kuehneosauridae) because of the special vertebral column and the long period of time in comparison with *Cteniogenys,* I therefore propose the new family Cteniogenyidae for unspecialized Eolacertilia.

C. *Macellodus* and *Saurillus*

1) Verification of the]genera

After a discourse with Prof. S. HENKEL and Prof. B. KREBS from the Institute for Paleontology of the F. U. Berlin, HOFFSTETTER (1964) has published the existence of scincomorph remains from the Portuguese coalmine Guimarota and referred to a possible relationship with the Purbeck formsof South-England, which were first described by R. OWEN in 1854 and 1855.

HOFFSTETTER's revision (1967) of the lacertilian material from the lowest Middle-Purbeck (mammalian beds) of Swanage relies on the numerous material of the BECKLES-collection in the British Museum, London (170 saurian specimens). In LYDEKKER's «Catalogue of the Fossil Reptilia and Amphibia in the British Museum, Part I» (1888) the following remains of the BECKLES-collection (purchase 1876) are labelled as «Species *Macellodus brodiei* OWEN 1855»: No. 48230-2, 48233, 48368, 48370, 48385. The catalogue No. 48233-DD now bears the new label R. 8242. This is a left dentary fragment 12 mm in length with 25 teeth resp. alveoli at least. The named specimen is not mentioned in HOFFSTETTER' publication (1967), although regarded by LYDEKKER (1888) as a typical specimen of *Macellodus brodiei* OWEN 1854.

The first description of lacertilians from the Latest Jurassic of Swanage resulted from the remains of the BRODIE-collection. This material, described by OWEN, 1854 and 1855 had never been in the hands of LYDEKKER, as the BRODIE-collection was not purchased by the British Museum before 1895, after the complection of LYDEKKER's catalogue. Certainly BRODIE has repeatedly given minor donations to the British Museum since 1853 (s. ZEUNER, 1939), but no Purbeck lacertilians were found among them.

In reviewing probably all the Purbeck material of the British Museum HOFFSTETTER (1967) misses BRODIE's finds described by OWEN and takes them to be lost.

In addition to the reptiles there also exist mammalian jaws in BRODIE's gathering at Durdlestone, which were turned up again at the Sedgwick Museum in Cambridge (CLEMENS, 1963). That these fossils have arrived at Cambridge is of no surprise

considering SEDGWICK as BRODIE's instructor, who was certainly provided with donations. Apart from the three registered mammalian remains, the curator Dr. FORBES could not find any other material of the RRODIE-collection at the Sedgwick Museum.
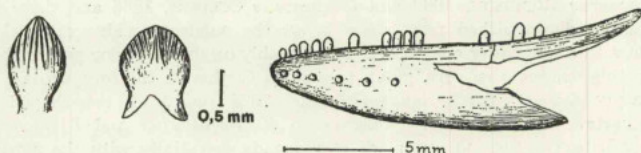

Fig. 9 — *Macellodus brodiei* OWEN, 1854, coll. BRODIE (after R. OWEN, 1854 p. 424, and 1861, pl. 8).
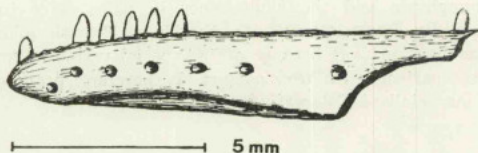

Fig. 10 — *Macellodus brodiei* incl. *Saurillus obtusus* after LYDEKKER [1888], Brit. Mus. R. 8242, coll. BECKLES («*Pseudosaurillus* or *Saurillus*» after a drawing by Dr. HENKEL and Dr. KREBS).
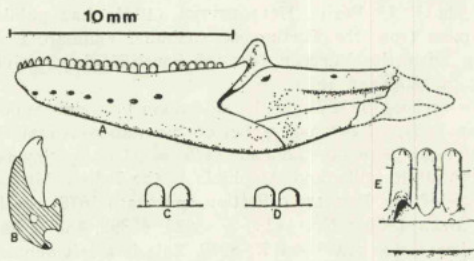

Fig. 11 — *Macellodus brodiei* after HOFFSTETTER, 1967 Brit. Mus. R. 8081, coll. BECKLES (after R. HOF-FSTETTER, 1967, p. 351).

Among the fossils of the BRODIE-collection at the Dorchester Museum there are no lacertilian remains, too. The British Museum only has three unimportant specimens, which had once been purchased with the BRODIE-assets.

By the genera *Macellodus* OWEN, 1854 and *Saurillus* OWEN, 1855 the authors OWEN, LYDEKKER and HOFFSTETTER mean disparates. With the lack of the types LYDEKKER thinks both genera identical and unites them with *Macellodus brodiei* OWEN, 1854. The missing type of *Macellodus brodiei* OWEN 1854, a ca. 25 mm long, with remarkable ventrally curved maxilla, is larger than the two paratypes, fragmentary dentaries (the well preserved one is ca. 17 mm long). After OWEN (1854, 1861) the three

specimens reveal a special dentition, apart from the size and shape of the jaw which differs from *Saurillus obtusus* OWEN, 1855 (type: a 10 mm long right dentary). The teeth of *Macellodus* are firmly attached in the alveoli, the crowns broad and laterally compressed, the cusps roughly rounded and slightly pointed, if unused. The name of the genus is explained by the spade-shaped teeth. The enamel has a special longitudinal striation. The base of the tooth is constricted facing the crown. OWEN has compared the teeth of *Macellodus* with those of *Hylaeosaurus* and *Echinodon* and distinctly illustrated the differences.

On account of the features of the type specimens from the BRODIE-collection (*Macellodus brodiei* OWEN, 1854) and the different jaws from the BECKLES-material, the union of the genera *Macellodus* and *Saurilus,* within the definition of LYDEKKER (1888), cannot be upheld. The specimen Brit. Mus. R. 8242 is due to compare with *Saurillus* OWEN, 1855 (p. 123) and *Pseudosaurillus becklesi* HOFFSTETTER, 1967.

To describ the neotype Brit. Mus R. 8182, coll. BECKLES as *Macellodus brodiei* OWEN, 1854 after HOFFSTETTER (1967) is not justifiable in my opinion ,as not corresponding with OWEN's description of *Macellodus*. Of the missing originals, the illustration of the 17 mm long dentary in OWEN, 1854 (p. 424) reveals a much longer superior suture with the surangular than the 14 mm long dentary of the neotype R. 8182, of which the inferior suture with the surangular and angular is obviously longer. As those sutures of bones are not plesiomorphously developed in the anatomic situations of the recent Lacertilia, the acute-angled kerf on the posterior part of the dentary has taxonomic signification. That is characteristic of Scincomorpha and for diagnostic use by the special development within this group.

After OWEN (1854, 1861) the teeth of *Macellodus* are obviously broad, stout, probably subpleurodont and bulging defined to the base of the tooth; with regard to the dimensions, HOFFSTETTER (1967) remarks «est suspecte (dents de 1 mm de diamêtre!)». The longitudinal striations of the enamel diverge laterally, but converge in the middle to the cusp.

2) *Macellodus* cf. *brodiei* OWEN, 1854

From the Guimarota mine three isolated teeth (Gui. L. 138, Gui. L. 139, Gui. L. 158) conform with the given anatomy of the teeth of *Macellodus*. A few similar ones are also present from the locality of Porto Pinheiro.

Diagnosis. — Broad spatulate teeth with longitudinal enamel striation, diverging laterally and converging to the cusp admedially.

Description and discussion. — The breadth of the three teeth from the Guimarota material corresponds with that of *Macellodus* OWEN, 1854 (0,8-1,0 mm). The teeth are used and therefore shortened (ca. 1 mm height). The fine enamel striae exist on both sides of the teeth, but they are much more slighly developed on the more convex labial side. The teeth have a minor pulp cavity. They are broken at the base (s. the waist of the specimen Gui. L. 138). The postulated real mitral form (or spadeshaped, spatulate) of the teeth differs from the neotype of HOFFSTETTER (1967) (Pl. I, 1, 2).

Macellodus brodiei OWEN, 1854 is identical with *Macellodon Brodiei* OWEN, 1861; that may be seen as a lapse of OWEN. In my opinion the three specimens of *Macellodus* described by OWEN, 1854 belong to different forms; surely the large maxilla opposite to the minor dentary fragments. The systematic position of *Macellodus* OWEN, 1854 can only be speculated. As the dentaries are broken at the posterior part, the position of the indicative sutures is doubtful. The rootlike base and the enamel morphology

of the teeth refer rather to a relationship with *Lisboasaurus* SEIFFERT, 1970 from the Guimarota, being related to the anguimorph *Dorsetisaurus* HOFFSTETTER, 1967 from Swanage.

The above nomenclaturally deserted neotype (Brit. Mus. R. 8182, coll. BECKLES) for *Macellodus* after HOFFSTETTER appears to be related to the specimen Brit. Mus. R. 8082 (*Becklesisaurus scincoides* HOFFSTETTER, 1967). There is only a difference in the size of the jaws; *Becklesisaurus scincoides* (R. 8082) is about two third larger than R. 8182 and R. 8081. The slender torsion of the angular, observed by HOFFSTETTER (1967) on the external side of the jaw R. 8082, is not delivered on the fragment R. 8182.

I suggest the following specimens of the BECKLES-collection Brit. Mus. R. 8182, R. 8081, R. 8099, R. 8113, R. 8120, R. 8184, R. 8197, R. 8204 (ascribed to *Macellodus brodiei* by HOFFSTETER) relate to the genus *Becklesisaurus* HOFFSTETTER, 1967. The Kimmeridgian vertebrate remains of Portugal include numerous fragments of comparable jaws.

3) *Becklesisaurus hoffstetteri* SEIFEERT, 1970

The species of the genus. — *Becklesisaurus scincoides* HOFFSTETTER, 1967 (p. 360-362) from the Purbeck of Swanage.

The species *hoffstetteri* is named after Prof. ROBERT HOFFSTETTER (Paris), who has described corresponding forms from the BECKLES-collection in the British Museum and named the genus *Becklesisaurus*. This species appears both in the Kimmeridgian of Portugal and in the Lower Cretaceous of Spain.
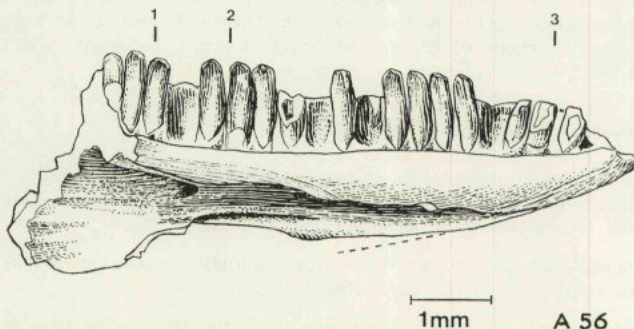

Fig. 12 — Gui. A. 56, *Becklesisaurus hoffstetteri*, left dentary (holotype), lingual view; between 1 and 2, the opening of the canalis alveolaris inferior can be seen, situated under the 17th tooth.

Diagnosis and discussion. — Dentaries with ca. 24 pleurodont, oblong teeth, of which the cusps lingually present a characteristic striation projecting as a cutting edge, and with an extending suture for an anterior elongated splenial.

The special morphology of the teeth of *Becklesisaurus hoffstetteri* has also been illustrated by HOFFSTETER (1967) for his «*Macellodus brodiei*» (R. 8182 and paratypes) and *Becklesisaurus scincoides* (R. 8082). Against the smooth convex labial side of the teeth, the lingual side presents a special enamed striation to the cusp. After the preliminary parallel run, two lingual edges converge to a prominent cusp; therefore

a smaller area between the edges is featured complying with the outline of the tooth, and the teeth achieve a chisellike aspect. in the anterior and mid part of the jaw the described cusp is not located on the middle of the tooth shaft, but eccentrically to rear, so that the edge of the superior tooth seems to be recurved. On the posterior teeth the cusp removes to the middle. The teeth have a cutting anterior, occlusial and posterior edge. The cusps are partly of light colour and transparent. The pulp cavity is
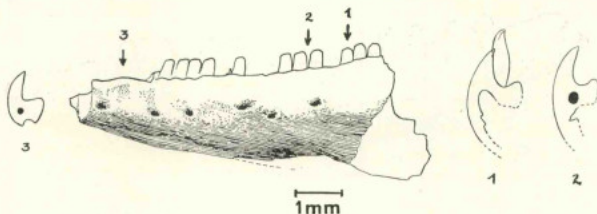

Fig. 13 — Gui. A. 56, labial view of the left dentary (holotype) of *Becklesisaurus hoffstetteri*. The cross-sections (1, 2, 3) show the development of the canalis alveolaris inferior.

relatively broad. Several teeth indicate an «iguanid» form of tooth replacement (after EDMUND, 1960, 1969) with a median basal fossa (s. the 17th tooth of the holotype Gui. A. 56). Basal foramina are in the middle of the tooth base. These features are to be found equally on *«Macellodus brodiei» after* HOFFSTETTER, 1967 and *Becklesisaurus scincoides* HOFFSTETTER, 1967. The dentary and the striation of the lingual tooth crowns are similar to the situation of the Upper Cretacious *Sauriscus cooki* ESTES, 1964 and
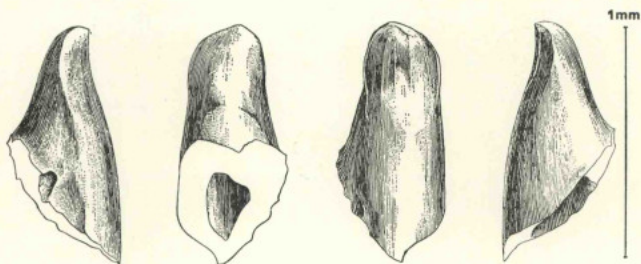

Fig. 14 — Gui. A. 56, tooth from the anterior part of the left dentary of *Becklesisaurus hoffstetteri* (holotype), from left to right: posterior, labial, lingual, anterior views.

of some species of the genus *Eumeces* (both genera are skinks). *Sauriscus* has in addition characteristic bifid teeth. The description of the dentary of *Sauriscus cooki* ESTES, 1964 conforms in a way with *Becklesisaurus hoffstetteri:*

«Posteriorly a deep notch for angula and surangular sets off a slender, pointed, dorsal coronoid process of the dentary, and a ventral angular process. There is the usual row of mental foramina. The Meckelian groove is quite restricted anteriorly, forming only a very shallow ventral groove. Posteriorly it enlarges and the internal mental canal opens under the nineteenth tooth. (— under the 18th tooth of 24 on

Becklesisaurus hoffstetteri Gui. A. 56 —) The type dentary bears twenty-seven teeth and in the other, somewhat smaller, specimens the number of teeth varies from twenty--three to twenty-five. The teeth are pleurodont, and project about one-fourth of their height above the parapet. The anteriorly broad subdental ridge thins out posteriorly and is separated from the teeth by a prominent subdental hollow. The teeth are closely spaced, subcylindric, slinghtly compressed at the crown, slightly inclined posteriorly»
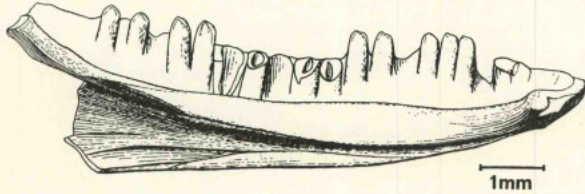

Fig. 15 — Gui. A. 45, *Becklesisaurus hoffstetteri;* in the row of teeth, the cusp is moving from behind to the middle of the tooth.

(p. 118); thereby the scincomorph character of *Becklesisaurus hoffstetteri* becomes distinct. At the base of the pleurodont attached teeth the lingual bony subdental ridge (regula subdentalis) forms a subdental hollow (sulcus subdentalis). This sulcus is typical of Scincomorpha (ESTES, 1964; HOFFSTETTER, 1967). The anterior broad subdental ridge thins out posteriorly making room for the splenial. The long attachment area for the splenial indicates an anterioly elongated splenial, which is not preserved
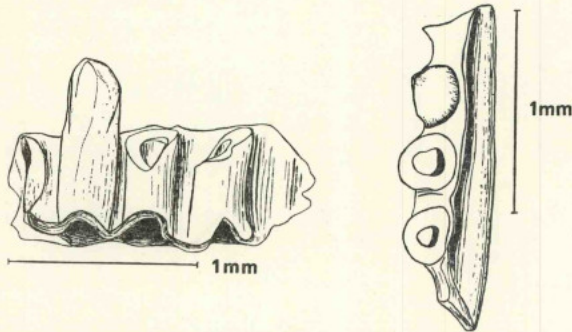
Fig. 16 — Gui. GE. 7, dentary fragment of *Becklesisaurus hoffstetteri* with a tooth, which has a distinct cutting edge and a lingual cusp.

on the Portuguese *Becklesisaurus.* The splenial closes the so-called Meckelian groove under the subdental ridge in large extention. This semicanalis or sulcus primordialis Meckeli includes in vivo the Meckelian cartilage and additionally in the posterior broadened part besides the vessels (A. and V. alveolaris inferior) the nerve alveolaris inf. (main branch of the N. mandibularis, V_3). The N. alveolaris inf. runs under the 18th tooth in a separate bony channel (canalis alveolaris inf.) and becomes parted from the supply of the teeth (plexus dentalis inf.) rami cutanei by ca. six foramina dento-facialia on the external side (labial) of the dentary (this allows

conclusions about the squamation and the salivary apparatus of the jaws, after OWEN, 1855, p. 123).

As represented by the Scincomorpha of the Guimarota and the recent *Chalcides chalcides,* also by *Saurillus* and *Pseudosaurillus* after HOFFSTETTER (1967, p. 356-360) the skinks and their related ancestors have developed a special attachment area for the muscle genioglossus on the ventral anterior part of the dentary. The M. genioglossus originates in the anterior lower margin of the dentary under the symphysis and reaches the ventral and lateral parts of the tongue. The muscle is used for the movement
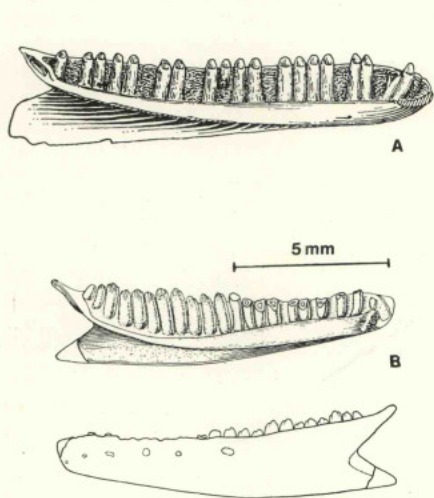

Fig. 17 — A: *Eumeces* cf. *fasciatus* (skink), Pleistocene of Florida, after W. AUFFENBERG, 1956, p. 165. B: *Sauriscus cooki* ESTES, 1964 (scincid), Lance-Formation, Upper Cretaceous, after R. ESTES, 1964, p. 118.
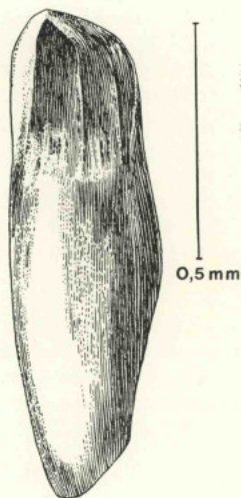
Fig. 18 — Gui. A. 56, tooth of *Becklesisaurus hoffstetteri* (lingual view) from the middle part of the left dentary (holotype), with pleurodont tooth attachment.

and protrusion of the tongue (s. BOBISON & TANNER, 1962; WETTSTEIN, 1931, 1932). *Becklesisaurus hoffstetteri* presents an extended, slender and notched attachment area for the genioglossus. The symphyseal region is relatively small, a feature also on the dentary Brit. Mus. R. 8099 (I class this specimen to the genus *Becklesisaurus* HOFF-STETTER, 1967). The development of the posterior part of the dentary of *Becklesisaurus hoffstetteri* is different to *Becklesisaurus scincoides* HOFFSTETTER, 1967 and *«Macellodus brodiei»* after HOFFSTETTER (1967). The superior process of the dentary to the coronoid, the processus coronoideus, rises dorsally on *Becklesisaurus hoffstetteri,* whereas on *«Macellodus brodiei»* after HOFFSTETTER (1967) and *Becklesisaurus scincoides* HOFF-STETTER, 1967 it is scarcely curved to the coronoid. *«Macellodus brodiei»* after HOFF-STETTER (1967) differs from *Becklesisaurus scincoides* HOFFSTETTER, 1967 apart from the size by the stronger development of the posterior ventral process of the dentary (processus angularis). Regarding the other conformity there are at the most presented two species of the genus *Becklesisaurus*. The coronoid of *Becklesisaurus hoffsteri* is

delivered only in fragmented bony remains on the processus coronoideus of the dentary Gui. A. 56; the anterior process of the coronoid has left behind a long attachment area on the lingual side of the dentary as on the related Purbeck forms from Swanage. As an ancestral feature of anguimorph habitus the sulcus primordialis Meckeli is very broad and large before the entry of the N. alveolaris inf. on the posterior internal side of the dentary. In the anterior part the sulcus runs diminishing to the ventral external side under the symphysis.

The maxillae of *Becklesisaurus hoffstetteri* are easily identified with the aid of the above described typical teeth. With the premaxillary teeth the number of the teeth in the upper jaw is multiplied contrary to that of the lower jaw. The left maxillae Gui. GE. 14 is associated with a fragment of the premaxilla, which has smaller teeth (s. also specimen P. P. I-L. 6). The following statement offers a rough survey of the allocation of the teeth in the upper and lower jaws of different lizards:

	premaxilla	maxilla	dentary
Tupinambis sp.	6	12/13	14/15
Lacerta lepida	7	21	26
Scincus scincus	2	19/20	20/21
Chalcides chalcides	3	14	16
Becklesisaurus hoffstetteri	4	21/22	23/24
Cordylus giganteus (*)	7	24	26
Varanus sp.	4	12	13
Iguana iguana	5	26	29
Pachydactylus bibroni (*)	9	32	32

(*) These statements are from EDMUND [1969].
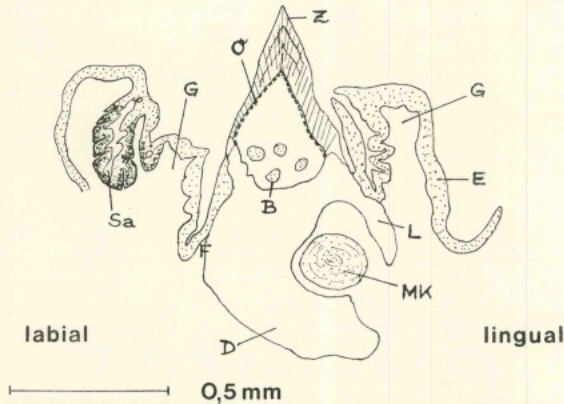
Fig. 19 — Cross-section of the dentary of a recent rhynchocephalian embryo, shortly to be hatched (modified after HARRISON, 1901 in WETTSTEIN, 1932, p. 172). B: Blood-vessels (A. and V. alveolaris inferior); D: Dentary; E: Epithelium of mucous membrane; F: Exit for cutaneous and salivary rami of the N. alveolaris inferior through Foramina dento-facialia; not cut in this section; G: Gingiva; L: Subdental ridge; MK: Meckelian cartilage in the Sulcus primordialis Meckeli; O: Odontoblast layer; Sa: Glands; Z: Tooth.

From the form of the maxilla (s. Gui. GE. 14, Gui. L. 31 and Gui. L. 34; similarly the right maxilla Brit. Mus. R. 8197 from Swanage) *Becklesisaurus* does not have a long snout, but rather a relatively short facial skull. The anterior part of the orbit is situated above the maxilla. A special curve of the posterior maxillary part indicates the onset of the jugal (s. Gui. L. 31, Gui. L. 56). The specimens Gui. 398 and P. P. I-L. 6 present the base of the naris. On the external side of the right maxilla Gui. L. 34 the dermal squamation has been traced. This bony ornamentation is also to be seen on the maxilla R. 8197 in the British Museum (published by HOFF-STETTER, 1960). Further more the external side of the maxilla presents numerous openings for the exit of the rami cutanei of the N. alveolaris superior (N. V_2).

The ornamental relief on the external side of the maxilla does not generally exist. The specimen Gui. L. 31 lacks it, whereas it is extraordinary well developed on the similarly formed maxilla Gui. L. 34. This attribute can be regarded as a sex- or race-feature.

The functional correlation of the characteristic teeth to the kind and form of the food, which certainly relates to be mobility of the tongue and the posteriorly risen coronoid (for the insertion of parts of the muscle adductor mandibulae), is not clear. Assuming a partial herbivorous alimentation it must be considered after OSTROM (1963):

«Since one of the principal saurian muscles (M. adductor posterior) that must be called into play in generating these mandibular grinding motions has its origin on the reptilian quadrate, effective grinding or mastication, other than a simple vertical chopping by repeated adduction, is precluded in the Squamata where the quadrate is free».

4) *Saurillus* cf. *obtusus* OWEN, 1855

From the same stratum of the ca. 115 m thick section in Durdlestone (Durlston, South-Swanage), where *Macellodus brodiei* OWEN, 1854 and mammalian remains had been found, a right scincomorph dentary of the BRODIE-collection was described as *Saurillus obtusus* by OWEN, 1855. After OWEN the stratum has the number K. 93 in AUSTEN's stratigraphical guide, described by different authors as 30-35 cm of thick limnetic marls (named «dirt bed, containing shells», «grey earthy, dirt bed», «marly freshwater shale with selenite, plant remains and vertebrates» or «mammalian beds» of the lowest Middle-Purbeck). The «dirt bed, containing shells» is not to be mistaken for a 10 cm stratum on the base of the Lower-Purbeck, which is known as «dirt bed, carbonaceous clay» (s. OWEN, 1871; SIMPSON, 1928).

The type specimen has «moderately long, conical, blunt-pointed teeth» (OWEN, 1855), which are neither broad nor flattened as of *Macellodus*. The external side of the 10 mm long dentary presents an acute-angled scincomorph, and a V-shaped configuration of the posterior end, where the surangular fits in. There are six foramina dento-facialia after OWEN (1855); the anterior openings are occasionally associated with a smaller one. The specimen R. 8130 from the BECKLES-collection of the British Museum corresponds in essential features with the type of OWEN, 1855 from the BRODIE-collection. Since the number of the teeth varies, the difference of 23 teeth on the dentary R. 8130 and at least 21 teeth of the holotype is insignificant, especially as the latter one is obviously a smaller individual. Because the holotype is not found today, the specimen Brit. Mus. R. 8130 should be considered as a type of an intimate relationship. For that HOFFSTETTER (1967) has created the new species *Saurillus robustidens* based on the supposed different number of the teeth on the specimen R. 8130 contrary to the lost original.

From the Guimarota material numerous remains can be attributed to the form *Saurillus obtusus* OWEN, 1855 (not HOFFSTETTER, 1967). But only one minor fragment
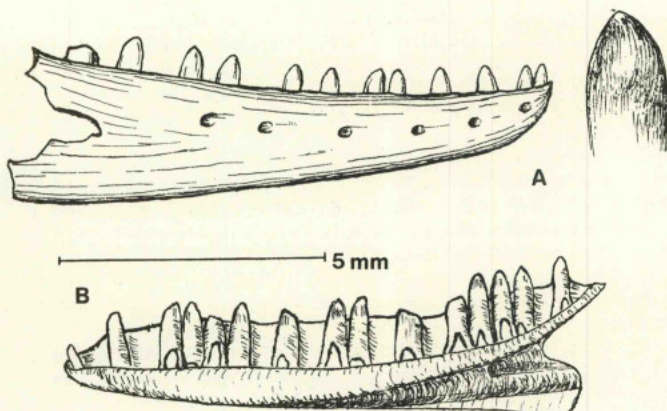
Fig. 20 — A: *Saurillus obtusus* OWEN, 1855, coll. BRODIE (after R. OWEN, 1855, p. 123). B: Brit. Mus. R. 8130, coll. BECKLES, *Saurillus robustidens* HOFFSTETTER, 1967; in contrast to OWEN's description of *S. obtusus* this right dentary does not bear Clunt teeth; lingually the teeth show a chisel-shaped cusp.
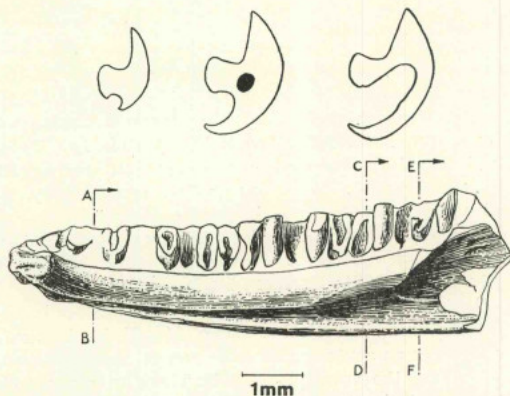
Fig. 21 — Gui. 5, right dentary of *Saurillus* cf. *obtusus* OWEN, 1855 (non HOFFSTETTER, 1967) from the Guimarota, lingual view; the cross-sections show the formation of the canalis alveolaris inferior.

with one tooth has come from the Upper Kimmeridgian of Porto Pinheiro (P. P. I-L. 4), which can be compared with *Saurillus obtusus* OWEN, 1855 (p. 123).

Diagnosis (s. OWEN, 1855) and discussion. — Dentaries with 22-23 conical, pleurodont teeth, the cusps of which are modestly curved lingualwards, and with a nearly straight and even thick subdental ridge, which dorsally develops an only a slightly indicated subdental hollow. A narrow Meckelian groove ventrally runs under the subdental ridge.

The specimen Gui. 5 equals the specimen Brit. Mus. R. 8130 from the relations of *Saurillus obtusus* OWEN, 1855 in many details. They differ by the configuration of the subdental ridge. The right dentary from the Guimarota is a little smaller than R. 8130. On both dentaries the N. alveolaris inf. enters approximately under the 18th
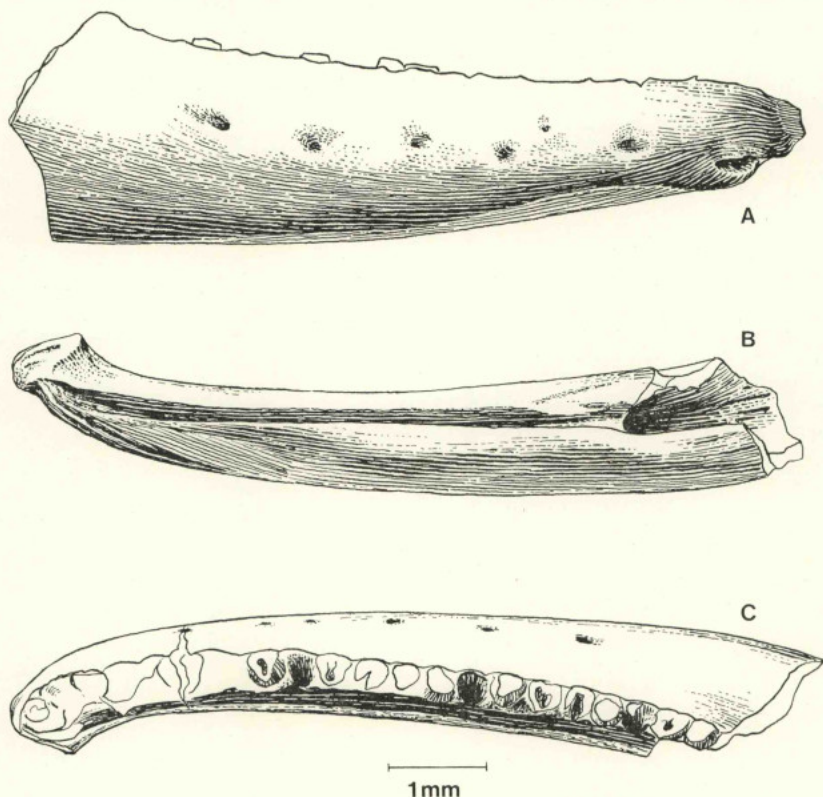

Fig. 22 — Gui. 5, *Saurillus* cf. *obtusus* OWEN, 1855, a right dentary from the Guimarota; A: labial view, in the anterior part the insertion of the M. genioglossus is ventrally marked; B: ventral view, straight run of the Meckelian groove; C: dorsal view, presence of a sulcus subdentalis.

tooth in the canalis alveolaris inf.; the heigh of the lower jaw measures 1,85 mm on the specimen Gui. 5 and 1,9 mm on R. 8130. The dentary of Gui. 5 might have born 22-23 teeth, the dentary R. 8130 presents 23 teeth. The partly preserved tooth fragments of Gui. 5 broken at the superior margin of the dental parapet. The teeth are closely placed, cylindric, conical; lingually the tooth cusp is chiselshaped, and on the tooth cross-section a narrow tubular pulp cavity can be seen. On the subdental ridge an attachment area for the splenial is to be seen under the 15th-20th tooth. This splenial mark is well preserved on several specimens of the Guimarota (Gui. 110, Gui. 255, Gui. 383). On the Guimarota specimens of *Saurillus* cf. *obtu-*

sus the posterior jaw bones are not present. The left dentary Gui. L. 29 indicates an acute-angled scinomorph limitation of the posterior end. The symphyseal region is developed as an approximately square swelling with a certain surface morphology, which has synchondrosially been connected with the pendant. The M. genioglossus has anteriorly left a muscle mark on the ventral external side of the dentary (on Gui. 5: 2,1 mm length and 0,3 mm breadth). As a primitive feature, a long and narrow Meckelian groove extends ventrally under the symphysis. The development of the subdental hollow is also ancestral. The Guimarota remains of *Saurillus* cf. *obtusus* present a variation of a distinguishable subdental hollow (Gui. 5, Gui. 419) to a distinct projected broad subdental ridge (Gui. 241, Gui. 322, Gui. 325). The thickness of the subdental ridge varies moderately, too. The subdental hollow is not yet developed on related ancestors, as may be seen on a comparable lacertilian dentary fragment from the Latest Bajocian (yielded by washing of the sapropelitic marls of the Causse du Larzac at Nant, Southern France). On the Middle Jurassic specimen the Meckelian groove also extends to the symphysis ventralwards.

The fragmentary maxillae Gui. 338 and Gui. 401 have the typical teeth of *Saurillus* (conical, blunt looking, externally convex and smooth, curved both lingual- and backwards, see also the dentary Gui. 223 and the fragment P. P. I-L. 4). The named maxillae are preserved with the anterior parts presenting a remarkable concavity for the naris (cf. the maxillae R. 8085, R. 8104 and R. 8118 from the BECKLES-collection of the British Museum).

The left dentary fragment Gui. 376 shows an abnormality anteriorly, where it is flexed off ventralwards without a spot of rupture. Since on the labial side a regeneration of the bone can be seen, a former violation of the lower jaw it may be supposed that it is due to.

From HOFFSTETTER's description (1967) in his *Paramacellodus oweni* the unity with *Saurillus robustidens* HOFFSTETTER, 1967 may be deduced. *Saurillus robustidens* R. 8130 is here reviewed as intimately related with *Saurillus obtusus* OWEN, 1855.

5) *Saurillus proraformis* SEIFFERT, 1970

Derivatio nominis. — *proraformis:* formed like the bow of a ship, referring to the appearance of the dentaries of the Kimmeridgian from the Guimarota.

Type species of the genus. — *Saurillus obtusus* OWEN, 1855 (non HOFFSTETTER, 1967) from the Purbeck of Swanage.

Diagnosis and discussion. — Relatively short, stout dentaries with 15-16 conical, pleurodont teeth, the cusps of which are a little curved back- and lingualwards; in addition the broad Meckelian groove totally runs on the lingual side of the dentary.

The pleurodont dentition presents closely placed, cylindric teeth with coniform cusps. The tooth crown is labially convex and lingually concave. The superior third surpasses the margin of the dental parapet; the pulp cavity is relatively broad. The entry of the canalis alveolaris inf. (for the N. alveolaris inf.) is located under the 11th-12th tooth. The canalis lies in the central dentary; therefore the foramina dento-facialia (mostly five) are approximately placed in the middle of the external side. The subdental ridge continually thins backwards; a distinct subdental gutter is developed. The relatively broad Meckelian grove extends on the internal side of the dentary, closed by the splenial (s. Gui. 49). By their height and breadth the dentaries appear to be compact. At the entry of the canalis alveolaris inf. the ca. 7 mm long dentary Gui. 7 has a height of 2,1 mm. The coronoid has three processes of the same length (s. Gui. 50), an anterior one to the dentary, a posterior one to the surangular and a dorsal
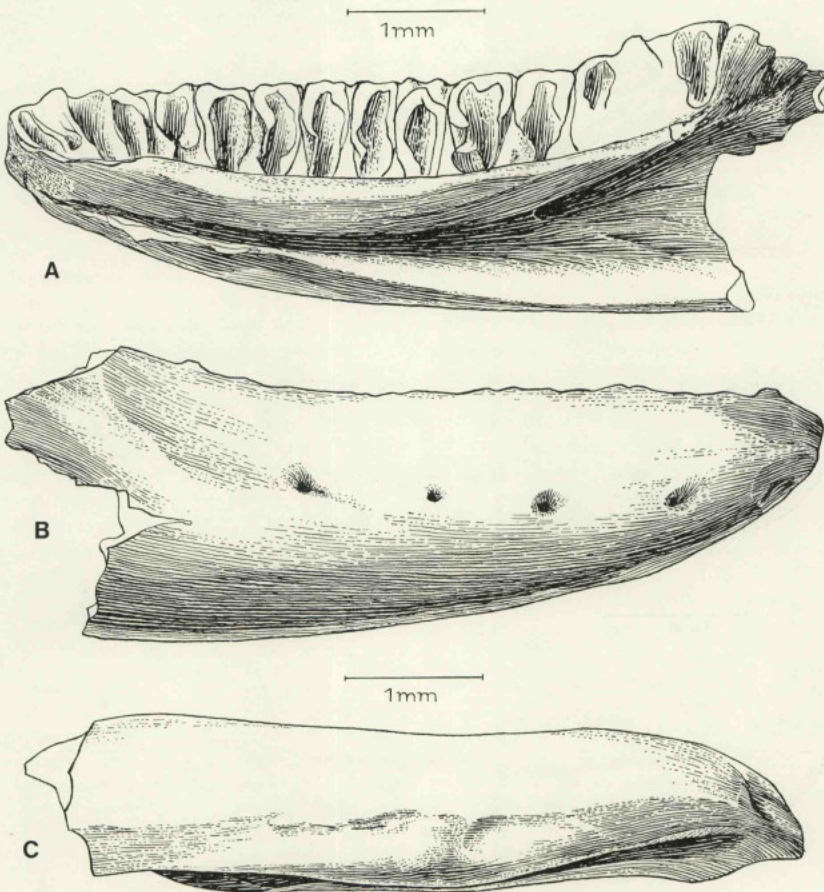
Fig. 23 — Gui. 7, *Saurillus proraformis*, right dentary (holotype); A: lingual view, posteriorly broad sulcus cartilaginis Meckeli; B: labial view, few foramina dento-facialia; C: ventral view, marks of muscle insertions.

one as processus massetericus for the insertion of the M. adductor mandibulae. The surangular is cuneiformly fitted in the acute-angled, scincomorph posterior part of the dentary. On the specimen Gui. 49 the suture is obliterated by coossification, indicating an adult individual. On the anterior external side of the surangular there is an opening, probably for the exit of a ramus of the nerve mandibularis (N. V_3). The angular mainly forms the ventral external side of the posterior part of the lower jaw (s. Gui. 49 and Gui. 50), whereas *Iguana* and *Varanus* show it located more on the ventral middle region of the jaw; on the latter one it is considerably reduced. The anterior end of the angular presents on the internal side of the jaw a foramen nervi mylohyoidei
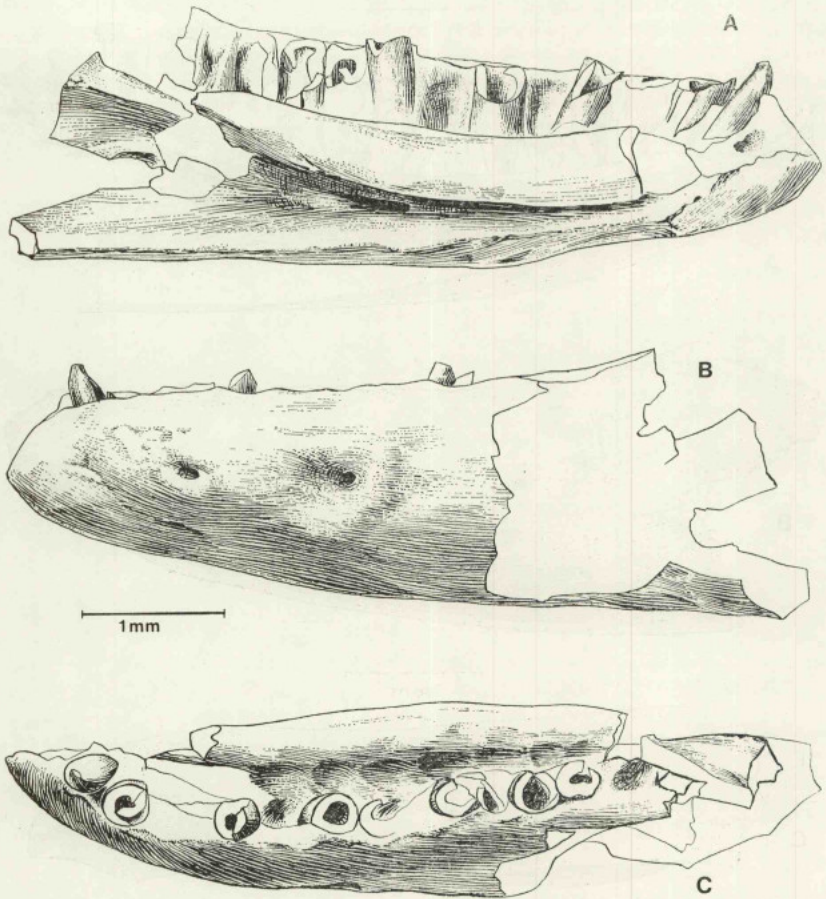
Fig. 24 — Gui. 10, left dentary of *Saurillus proraformis* from the Guimarota; A: lingual view, large
Meckelian groove; B: labial view, few foramina dento-facialia; C: dorsal view,
distinct sulcus subdentalis.

(a ramus of the N. V₃ for the motorial innervation of the M. mandibulohyoideus III
after ROBISON & TANNER, 1962) under the suture to the splenial. This feature is
obviously plesiomorphus (s. HOFFSTETTER, 1967), but the other described features are
characteristic of the Scincomorpha.

A long, slender, oval fossa Meckeli exists on the internal side of the lower jaw
(for the taking up of the N. mandibularis). The fossa Meckeli is formed by the suran-
gular and gonial-articular. On the specimen Gui. 50 the gonial (= prearticular after
WILLISTON, the seventh bone of the lower jaw) is apparently not yet tied to the

articular. That gonial is distinguished by a ventral rough area on the posterior internal side, which is caused by the insertion of a strong M. pterygomandibularis (s. WETTSTEIN, 1931; ROBISON & TANNER, 1962). Regarding the relatively large breadth and length of the muscle insertion a powerful masticatory and grinding movement is to be assumed for the consumotion of consistent food.

The processus retro-articularis is fragmentary presented on the specimens Gui. 49 and Gui. 50. It is only a little ventrally inclined and has a distinct fossa retro-articularis, ahead of which the fovea articularis is located for the articulation with the condyle mandibularis of the quadrate. In the interior of the fossa retro-articularis there are two separated little foramina, a third opening externally lies on the posterior internal side of the processus retro-articularis.
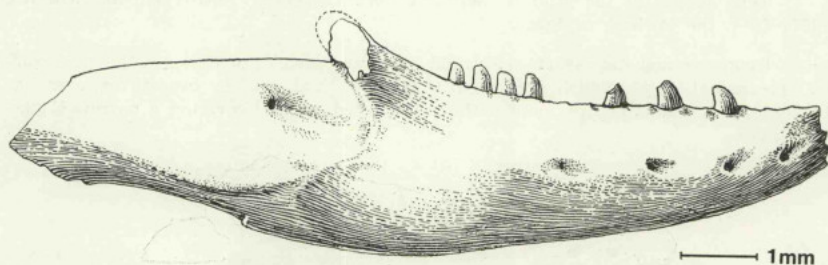

Fig. 25 — Gui. 49, *Saurillus proraformis*, fragment of a right lower jaw; the dentary is co-ossified with the surangular, which locks into the posteior end of the dentary, acute-angled; in the surangular the foramen antero-externum is present (exit of the SIEBENROCK's nerve after HOFFSTETTER, 1967).

The maxillae of *Saurillus proraformis* are easily identified by their morphology and the low number of teeth (s. Gui. A. 75). A long attachment area for the jugal is present. From a large extending posterior concavity of the maxilla (s. Gui. 335, Gui. A. 75 and Gui. A. 87) an orbit located above the posterior part of the maxilla and a short snout can be concluded, also indicated by the compact dentaries.

Above the fossa Meckeli a nerve channel (for SIEBENROCK's nerve after HOFFSTETTER (1967), a ramus of N. V_3) runs in the surangular, with the exit on the anterior side. The foramen antero-externum supraangulare is found in the posterior extension of the cuneiform anterior part of the surangular. In this anatomical position it is only known of Scincidae and Gerrhosauridae; in addition *Xantusia riversiana* can be compared.

As distinguished from the gerrhosaurids the splenial of *Saurillus proraformis* has no process to the coronoid, which represses the anterior side of the processus dentalis on *Gerrhosaurus*, but the splenial leavelike fits in the Meckelian groove, so that the processus dentalis is attached with a large inferior margin as on scincids and lacertids. Whereas on *Gerrhosaurus* the processus supraangularis of the coronoid extends to the fossa Meckeli and the prearticular, it is not elongated on *Saurillus proraformis*, but approximately equal in length as the processus dentalis; that is the case with the Scincidae, too.

On the jaws of cordylids the processus retro-articularis is emphasized and ventrally inclined, on those of *Saurillus proraformis* it is scarcely so. A farther difference is the development of the splenial extending to the external side of the lower jaw of cordylids, but not of *Saurillus. Saurillus proraformis* differs from the Lacertoidea by the existence of a distinct subdental hollow and the absence of a long fourth coronoid

process to the external side of the dentary. The genus *Saurillus* represents an ancestral form of the Scincidae.

6) *Saurillus henkeli* SEIFFERT, 1970

This form is closely related with *Saurillus proraformis*, having differences in the proportions of the lower jaw. The dentary is rather straightly stretched and not shaped like a bow. Hitherto this species is only known from the Guimarota mine.

Derivatio nominis. — *henkeli:* after Prof. SIEGFRIED HENKEL (Berlin), who has carried out the recovery of the fossil vertebrates from the Guimarota.

Type species of the genus. — *Saurillus obtusus* OWEN, 1855 (non HOFFSTETTER, 1967) from the Purbeck of Swanage.

Diagnosis and discussion. — Straight extending, slender dentaries with ca. 15 conical, pleurodont teeth, which are slightly recurved and project two difths over the border of the dental parapet, and with an elongated splenial covering a narrow Meckelian groove.
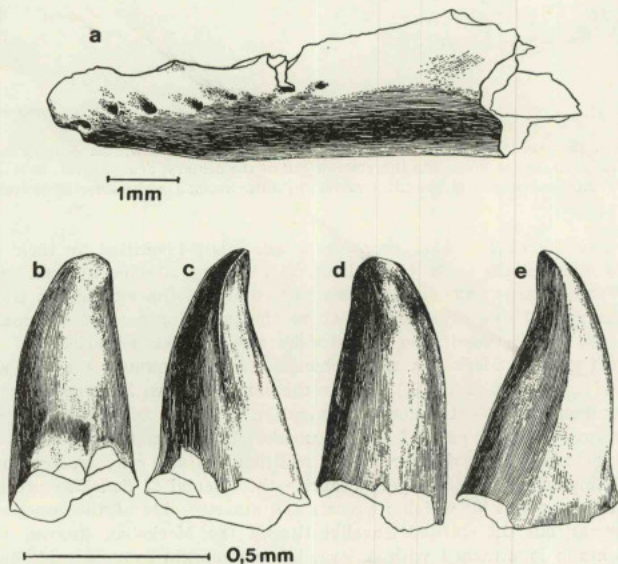
Fig. 26 — Gui. 6, *Saurillus henkeli*, left dentary (holotype); a: labial view, a row of foramina dento-facialia; b-e: one tooth of the specimen, b: labial, c: posterior, d: llingual, e: anterior view.

The lower jaw of *Saurillus henkeli* has a remarkable similarity with that of the recent *Chalcides chalcides*. The inferio margin of the slender dentary runs almost straight as that of the subterrestric living skink *Chalcides*, the skull of which is flattened for burrowing (s. HAAS, 1936). The straightly running subdental ridge considerably thins backwards; a distinct subdental hollow is developed. The posterior process

of the coronoid to the surangulalr presents a strong, medially directed crest (Gui. 28). The posterior part of the lower jaws is slim; internally there is a long furrowlike fossa Meckeli between the surangular and gonio-articular as on *Chalcides, Scelotes, Chamaesaura* and *Pseudocordylus;* but opposite to the cordylids the processus retro-articularis of *Saurillus henkeli* is not prominently inclined ventrally. On the ventral internal side of the gonio-articular the insertion area for the M. pterygomandibularis is less marked than that one of *Saurillus proraformis.*

The maxillae are of fragile structure (Gui. 292, Gui. L. 27, Gui. L. 173). The openings of the exit for the rami cutanei of the N. alveolaris superior (N. V_2) are located closely above the maxillary crest obviously confined to this straight row. This habitus is found on *Pseudosaurillus becklesi* HOFFSTETTER, 1967 and «*Saurillus obtusus*» after HOFFSTETTER (1967), non OWEN, 1855, also on the recent *Chalcides chalcides.* From the limitations of the maxillae and the dentaries a short facial skull can be assumed. The specimen Gui. 254 (a left premaxillary fragment) reveals pairs. The premaxilla bears four teeth, like *Chalcides.* The morphology of the skull with the straight and slender lower jaw suggests the presence of a burrowing skink.

The postcranial skeletal remains (Gui. L. 30) offer the expected morphological features in comparison with the skeletons of *Chalcides chalcides* and *Chalcides guentheri.* The limbs are on the point of being reduced as may be seen by the shortened femur. As for the support of the vertebral column, a zygosphene-zygantrum-articulation is developed for additional winding locomotion. Seven vertebrae with ribs, a femur a humerus, a tibia with fibula are collected on the piece Gui. L. 30. The colour and the consistence of the bony remains of *Saurillus henkeli* corresponds with that of the postcranial skeleton Gui. L. 30 (s. also the chapter about the forelimbs).

Annotation. — As «*Saurillus obtusus*» after HOFFSTETTER (1967), non OWEN, 1855 and *Pseudosaurillus becklesi* HOFFSTETTER, 1967 are only different in the size, they are to be considered for the present as being congenerically related. The jaw remains of these Swanage forms are distinguished by numerous slim, conical teeth (ca. 30 pleurodont teeth on the dentary).

D. *Lisboasaurus* SEIFFERT, 1970

1) *Lisboasaurus estesi* SEIFFERT, 1970

HOFFSTETTER (1967) describes an anguimorph lacertilian genus from the lowest Middle Purbeck of Swanage, *Dorsetisaurus purbeckensis,* which is characterized by lanceolate teeth:

«La couronne, revêtue d'un email très brillant, est comprimée, avec des bords tranchants convergeant en une pointe légèrement déjetée vers l'arrière. On observe une certaine hétérodontie: les dents antérieures sont plus élancées, les postérieures plus larges et moins aigues. Ces dents sont creuses, et, de ce fait, leur partie comprimée est souvent écrasée lors de la fossilisation.» (HOFFSTETTER, 1967).

Derivatio nominis. — *Lisboasaurus:* this lacertilian is named after the capital of Portugal, following the geographical derivatio of the name *Dorsetisaurus* HOFFSTETTER, 1967, to which the new genus is related. *estesi:* after the paleoherpetologist Prof. RICHARD ESTES (Boston), who has recognized first (on visiting Berlin in 1967) the relationship of the Guimarota genus with the English form *Dorsetisaurus.*

Lisboasaurus is represented by several bony remains and isolated teeth from the Kimmeridgian of Portugal.

Diagnosis of the genus. — *Lisboasaurus* has lanceolate teeth with a root-like teeth base («mosasauroid»), a lingual cusp and a special enamel gloss.

Diagnosis of the species. — The species is characterized by labio-lingually compressed, smooth teeth, the bulgy bases of which are lingually linked by a mediana groove, which continues on the inferior part of the tooth. The maxilla has a relatively long prefrontal process and a longer, broad jugal process; between them an anteriorally shifted notch exists for the attachment of the prefrontal. There are divisions for at least 15 teeth, the first of which has obviously been very enlarged.
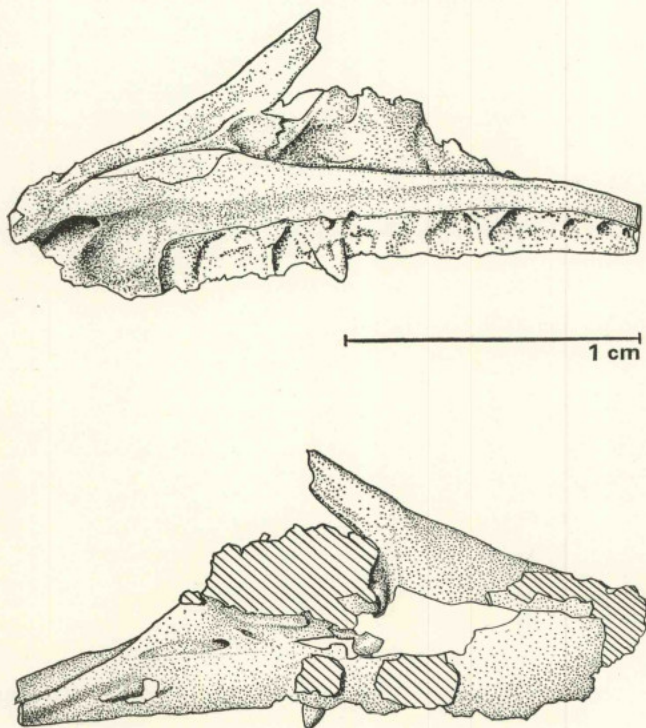

Fig. 27 — Gui. 37, *Lisboasaurus estesi,* right maxilla (holotype); above: lingual view, the preserved tooth shows a grooved, bulgy base with a pleurodont mode of attachment; below: labial view.

Discussion. — The extraordinary form of the dentition of *Lisboasaurus* manifests a similarity with that of the Lower Cretaceous Aigialosauridae and the Upper Cretaceous Mosasauridae. The aigialosaurid with the best known dentition is *Opetiosaurus bucchichi* KORNHUBER, 1901 from the Lower Cretaceous of Lesina, Dalmatia; KORNHUBER describes:

«Jede Zahnkrone ist nämlich von einem Sockel, d. i. von einem knöchernen Säulchen oder einer Stütze, von durchschnittlich 5 mm Höhe, getragen, dem sie, genau abgegrenzt und von einer zarten, wallartigen Erhöhung umgeben, aufsitzt. Der Sockel ist cylindrisch und endet, nach oben sich etwas verschmälernd, stumpf conisch mit der

kreisförmigen Ansatzstelle des Krönchens. Die Seite des Sockels ist schwach gestreift, in der Mitte mit einer deutlichen, rinnig vertieften Längsfurche versehen, die fast den vierten Theil von der Sockelbreite einnimmt. Die Zahnkronen haben durchschnittlich 2 mm Durchmesser an ihrer Basis und über 3 mm Höhe; sie sind mit ihrer kegelförmigen Spitze etwas nach hinten gekrümmt und von einem glänzenden, bräunlichen Schmelze überzogen, der keine Zähnelung, sondern nur eine schwache Streifung erkennen läβt... Die beschriebenen Sockel sind dem Kieferrande aufgewachsen und scheinen etwas in die Unterlage eigesenkt zu sein.»

The big aquatic mosasaurs with secondary subthecodontly fixed teeth (s. McDowell & Bogert, 1954) are presumably derived from the aigialosaurids. There is a convergence to the mosasaurs in the jaw construction and the dentition by the toothed birds Hesperornithiformes from the Upper Cretaceous of North America (s. Marsh, 1880; Kornhuber, 1901; Gregory, 1951, 1952). By Gregory (1952) the lower jaw of *Ichthyornis* Marsh, 1873 have been emended as jaw remains of a small mosasaur. The adaptation to the aquatic, piscivorous mode of life of the Mosasauridae and Hesperornithiformes has caused the similar opportune phenotypic features to evolve. For the aigialosaurids Kornhuber (1901) accepts the tooth structure of mosasaurs described by Cuvier. Accordingly the base of the tooth is only hollow in the period of increase; it becomes completely solid. At first the teeth are joined by connective tissue, then coossify with the jaw by means of a bone-like substance resembling the cementum dentis. Contrary to the mammalian teeth the «mosasauroid» teeth have no roots of dentine covered with cement. To exclude mistakes the special base of «mosasauroid» teeth is better termed as a socle, not as a root.

From the Guimarota no emitted solid teeth of *Lisboasaurus estesi* with a resorbed base have been found. The mode of attachment on the jaw is pleurodont despite the special socle (Gui. 37). The tooth base of *Lisboasaurus estesi* has a longitudinal groove like *Opetiosaurus*. Therefore on the lingual side the teeth seem to be seated on double-socles. The alveoli present a distinct concavity as *Dorsetisaurus purbeckensis* Hoffstetter, 1967. The description of the dentition of *Dorsetisaurus* corresponds on the whole with that of *Lisboasaurus;* in lieu of the special development of an tooth socle with a median longitudinal groove, on *Dorsetisaurus* an enlarged tooth base is formed with a medial foramen, creating the impression of a furrowy base. Because of the relationship in the tooth structure and attachment *Dorsetisaurus* and *Lisboasaurus* presumably have derived from common ancestors. The maxilla of *Dorsetisaurus* differs from that of *Lisboasaurus estesi,* which instead of an anterior nasal concavity has a considerably straight dorsal bony margin like *Varanus* sp. and some amphisbaenids. With the heterodonty and the connection to the prefrontal the maxilla forms a relationship with the situations on the amphisbaenid *Rhimeura matcherii* Baur, 1893, Oligocene.

The deformed skeletal remains Gui. L. 177 offer an unpaired diagenetically distorted fragmentary frontal, a broad fragmentary parietal, a broad quadrate, a strong pterygoid, and badly preserved fragments of the lower jaw, procoelous vertebrae and ribs. The strong procoelous vertebral centrum (s. Gui. L. 177) has a relatively big condyle, also laterally an oval articular facet for an unicipital rib. The habitus is distinctly anguimorph. In the posterior part of the vertebra a strong spina dorsalis rises oar-blade-like dorsalwards (Gui. L. 33).

Annotation. — For *Dorsetisaurus* Hoffstetter (1967) has nominated the new anguimorph family Dorsetisauridae, which are classed to the Anguoidea; but he accentuates chiefly non-anguid pronounced features (p: 364 and 369). Because of the tooth construction and the maxillary shape *Lisboasaurus* can be added to the Varanoidea. A relationship with *Dorsetisaurus* can be found by the characteristic tooth morphology.

2) *Lisboasaurus mitracostatus* Seiffert, 1970

Derivatio nominis. — *mitra:* mitriform; *costatus:* groined; the name of the species refers to the mitral form of the teeth with a lingual enamel fluting.

Type species of the genus. — *Lisboasaurus estesi* from the Kimmeridgian of Portugal.

⊢——————⊣ 1 mm
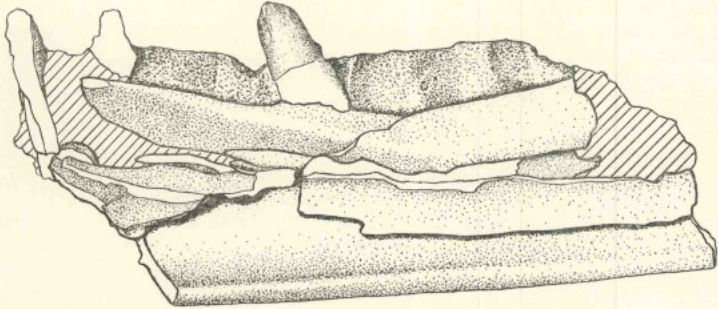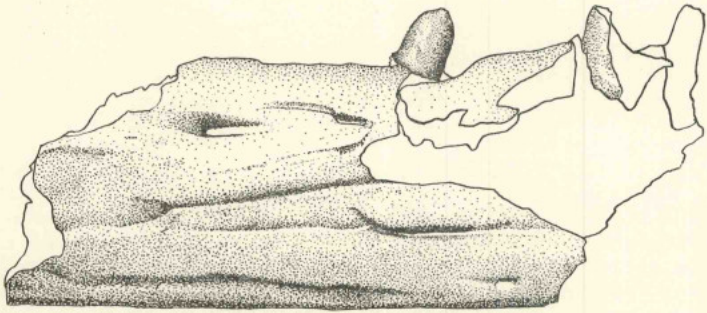

Fig. 28 — Gui. 34 — *Lisboasaurus mitracostatus,* fragment of a left dentary (holotype); above: lingual view; below: labial view.

Diagnosis. — The jaws have mitral pleurodont teeth with a socle and with a lingual cusp, which is fortified by a medial enamel rugosity and accompanied by some lateral flutes. The external side of the jaw presents numerous foramina and short, narrow channels.

Discussion. — The material of *Lisboasaurus mitracostatus* consists of some small jaw fragments and isolated teeth presenting a heterogeneity. The emitted solid teeth are without socle; therefore they are relatively short and mostly rather broad. The lingual cusp of these teeth is dorsally set off and often shifted backwards, so it is distinguishable to which side the jaw belongs. Partly the toothed jaw remains distinctly differ in tooth breadth and thickness of the enamel rugosity. From the different development of the teeth I had proposed two subspecies in 1970, but probably these forms (*L. mitracostatus mitracostatus* and *L. mitracostatus lacinianus*) are only on another place located ingredients of integral jaws. *Lisboasaurus mitracostatus* differs from *Lisboasaurus estesi* by the enamel rugosity. *Lisboasaurus estesi* has nearly smooth teeth and a distinct socle groove. The base of the teeth of *Lisboasaurus mitracostatus* seems to be affixed subthecodontly. The teeth of both species are labio-lingually compressed.
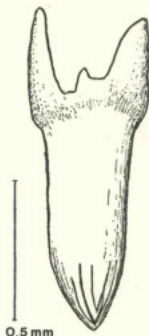

Fig. 29 — Gui. 24, tooth from a maxillary fragment of *Lisboasaurus mitracostatus*, lingual view. The teeth have a socle which has been put in the maxilla (resp. in the jaw). The tooth reveals a pleurodont attachment. The upper lingual tooth part is ribbed and shows a lingual cusp.

The jaw remainder Gui. 24 presents a little replacement tooth in one alveolus; EDMUND, 1969 on «mosasauroid» teeth:

«The replacement tooth develops distolingually to the crown of its predecessor on the surface of the bone near the alveolar margin. This area of bone and the base of the tooth become deeply resorbed, and the replacement migrates into a cavity in the base where it grows to a large size before the loss of the old crown.»

The old tooth above the replacement tooth is the largest one and distinctly offset for use in comparison with the other ones. Below the other delivered teeth there do not exist any more replacement teeth, therefore a wavelike replacement can be assumed.

The channelled structure on the external side of the jaw (s. Gui. A. 15) is probably to be referred to as the dermal squamation. Contrary to *Lisboasaurus mitracostatus* the external side of the jaw of *Dorsetisaurus purbeckensis* HOFFSTETTER, 1967 is not channelled; in the herpetology the features correlated with the squamation are significant in separating the species. A similar channelling on the labial side is to be seen on *Cteniogenys reedi*.

The following anguimorph features are to remark:

a) the solidity of grown out teeth with a filled base;
b) the lack of a subdental gutter and of an internal opening for the N. alveolaris inf., which runs in the sulcus primordialis separated of the Meckelian cartilage by a bony intramandibular septum [after ESTES, 1964];
c) the lack of a bony roofed superior temporal opening;
d) the fusion of skull bones, an unpaired parietal, fused frontals and premaxillae;
e) the Meckelian groove is located ventral anteriorly and not covered by the splenial there.

Annotation. — The teeth of *Lisboasaurus mitracostatus* have a similar morphology (cf. P. P.-L. 26) as those of *Macellodus brodiei* OWEN, 1854, which is different by spatulate teeth and special directed enamel striae.

E. *Introrsisaurus pollicidens* SEIFFERT, 1970

Derivatio nominis. — *introrsus:* turned inwards; *pollex, pollicis:* thumb; the name refers to the morphology of the teeth, which are inclined lingualwards like a thumb with the nail side.
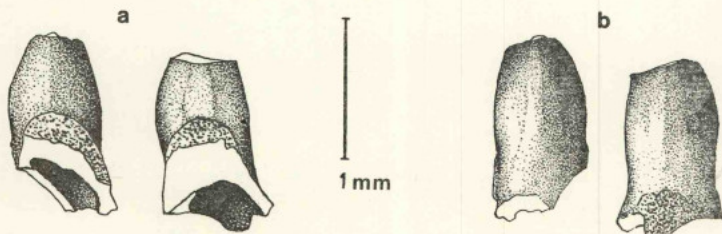

Fig. 30 — Gui. A. 73, teeth of *Introrsisaurus pollicidens;* a: labial view, base showing surface of contact for the pleurodont attachment at the dentary; b: lingual view, curved inwards (lingualwards) with a median elevation.

Diagnosis. — Pleurodont attached teeth with a crown little broadened, which is inclined lingualwards looking like a finger end. The labio-lingually compressed crown is labially convex, lingually the tooth presents a basi-occlusially running medial elevation. Thereby the tapered sides of the tooth are distinctly set off.

Discussion. — This form is only represented in the Guimarota material with the specimens Gui. 43, Gui. A. 73 and Gui. L. 232. The jaw fragment Gui. L. 232 is light brown, a foramen dento-faciale is preserved. Alveoli are obviously not present. The tooth of Gui. L. 232 is red-brown coloured, whereas the teeth of Gui. A. 73 are dusky because of more intense chemical reactions. On the lingual surface of the teeth a fine striation is visible. The teeth appear to be obliquely implanted and slightly recurved backwards. The evidence on *Introrsisaurus pollicidens* is limited by the incomplete delivery. The description of the teeth of *Coniosaurus crassidens* OWEN, 1851 (id. Coniasaurus) from the Upper Cretaceous of Europe by OWEN (1851) and NOPCSA (1908) corresponds to a certain degree with *Introrsisaurus pollicidens:*

«Die Zähne sind dem Kiefer pleurodont aufgesetzt und unterscheiden sich durch den Mangel eines Sockels von den Zähnen der Aigialosauriden oder Mosasauriden. Sie sind an ihrer Basis kontrahiert und genau so dem Kieferknochen aufgesetzt, wie man dies bei den hinteren stumpfen Zähnen von *Varanus niloticus* antrifft. Die poröse kanal durchzogene Knochensubstanz ist bei beiden Formen ebenfalls die gleiche... Die vorderen, stumpfkonischen, im Querschnitt runden Zähne zeigen in ihrer Mitte bloß eine kleine Aufblähung und an ihrem Vorderteile einen markiert vorspringenden Flügel, der jedoch nicht bis an die Krone heranreicht und an den weiter hinten gelegenen Zähnen an Größe zunimmt.» (NOPCSA, 1908, p. 57-58).
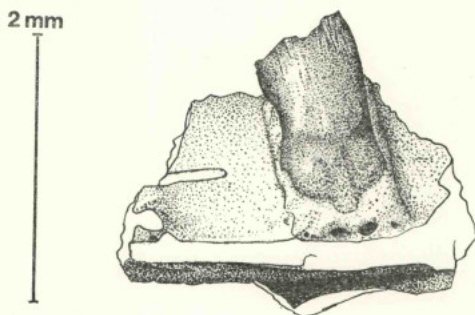

Fig. 31 — Gui. L. 232, *Introrsisaurus pollicidens,* recurved tooth with broken top, pleurodont attachment presumably fragment of a left dentary).

The systematic position of *Coniosaurus* is uncertain; the form is classed to the dolichosaurids or the aigialosaurids (by KUHN (1963) to the Iguania).

The described lacertilian material from the Kimmeridgian of Portugal is probably distributed on the following systematic categories:

Infraordo. — *Eolacertilia*
    Cteniogenyidae
        Cteniogenys reedi SEIFFERT, 1970

Infraordo. — *Scincomorpha*
    Scincidae
        Becklesisaurus hoffstetteri SEIFFERT, 1970
        Saurillus cf. obtusus OWEN, 1855
        Saurillus proraformis SEIFFERT, 1970
        Saurillus henkeli SEIFFERT, 1970

Infraordo. — *Anguimorpha*
    Dorsetisauridae
        Lisboasaurus estesi SEIFFERT, 1970
        Lisboasaurus mitracostatus SEIFFERT, 1970
    Dolichosauridae
        ?Introrsisaurus pollicidens SEIFFERT, 1970

Incertae sedis
        Macellodus cf. brodiei OWEN, 1854.

F. The bones of the skull

1) Os parietale

a)   Specimens Gui. 82, Gui. L. 14: paired parietals with relatively long processus parietales. The pineal foramen is presumably situated between the frontals and the parietals. The fact that they are in pairs indicates that the specimens belong to the eolacertilian form of Guimarota.

b)   Specimens Gui. 170, Gui. L. 22, Gui. L. 25, Gui. L. 42, Gui. L. 52, Gui. L. 53: relatively thick unpaired parietals, looking robust and sturdy. On the inferior side strong lateral ridges accentuate a large cavity of the cranium in the parietal. On the dorsal side a special relief is developed, known of Scincidae and Lacertidae. The osteodermally formed squares resemble that of *Lacerta lepida* and also of *Chalcides chalcides*. There exists a minute parietal foramen. The irregular lateral borders of the parietal indicate a secondary annexation of dermal bones, which close the supratemporal opening
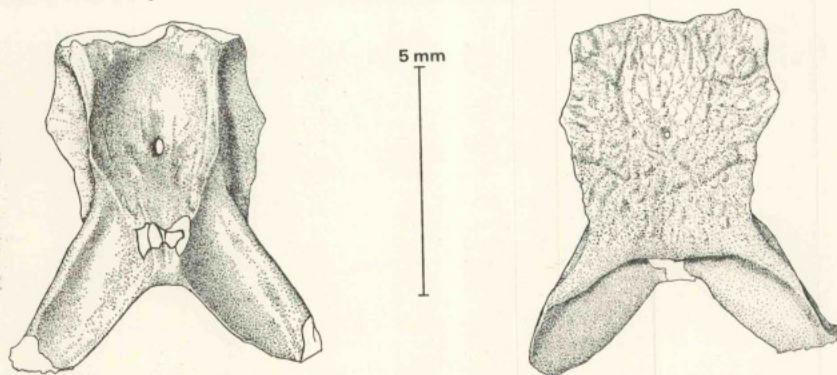

Fig. 32 — Gui. 170, scincomorph parietal with a small centric foramen; right: dorsal view, surface pattern produced by the scutes; left: ventral view.

(a scincomorph feature). On the posterior part of the processus parietales, there is a notch for the attachment of the squamosal; that refers to the hockey-stick shape of the squamosals. The internal side presents extended, slender impressions of the hemispheres. In the posterior part of each side a short ridge branches off medially from the internal lateral borders; this one connects with the processus anterior of the tectum synoticum (BARROWS & SMITH, 1947). Both ridges converge on a median swelling on the posterior end of the parietal; the latter is notched to connect with a dorsal supraoccipital process. Corresponding situations are found on Cordylidae (by McDOWELL & BOGERT, 1954) and Xantusiidae (by BARROWS & SMITH, 1947). On Lacertidae a homologous sagittal ridge is developed, which includes a foramen for the cartilaginous rest of the processus ascendens tecti synotici (s. HAAS, 1936). On some Scincidae only this foramen exists, but very distinctly.

c)   Specimens Gui. 75, Gui. L. 28, Gui. L. 43, Gui. L. 141, Gui. GE. 12: unpaired parietals with straight lateral borders, which converge slightly behind. The dorsal surface is nearly smooth and only a very sparse pattern is suggested (Gui. GE. 12). A median parietal foramen is distinctly developed. On the posterior transversal margin of the parietal there is a median process, which is emphasized by two lateral dents;
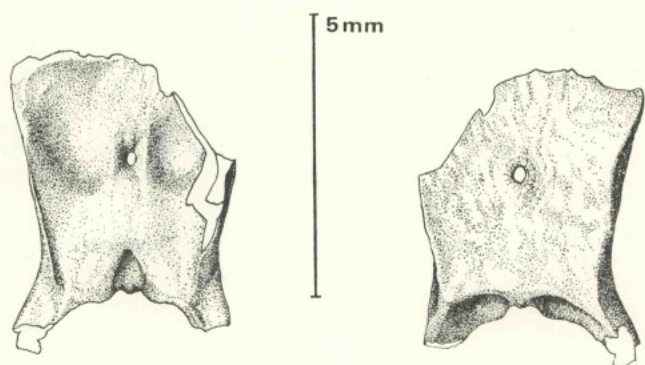
Fig. 33 — Gui. GE. 12, parietal of a scincid with a nearly smooth dorsal surface; left: ventral view; right: dorsal view.
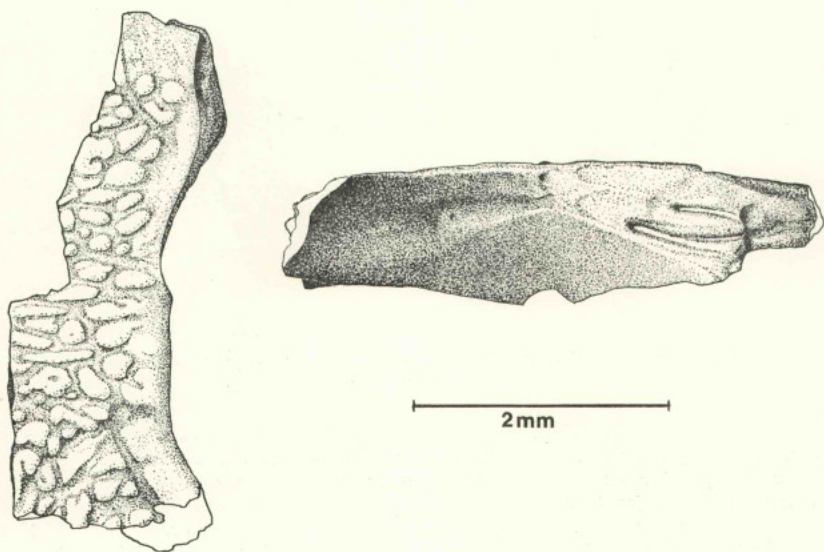

Fig. 34 — Gui. 171, right frontal element with a dorsal surface granularly patterned; left: dorsal view, in the anterior part a lateral area of contact for the the right prefrontal; right: lateral view, dorsal orbital border.

that is the connection point with the supraoccipital. On the internal side posteriorly, a fossa is to be seen, opening backards, which is partly filled with the cartilaginous rest of the processus ascendens tecti synotici (after HAAS, 1936), which becomes the supraoccipital posteriorly (s. Gui. L. 43, Gui. GE. 12). These features are found in the family Scincidae.

d) Specimens Gui. L. 23, Gui. L. 40, Gui. L. 41, Gui. GE. 9: unpaired, relatively broad parietals with a distinct relief, which does not reveal any clear arrangement of squares. A central parietal foramen is present. The ventral side is prominently formed. The connection with the supraoccipital is only weakly indicated.

e) Specimen Gui. L. 44: an unpaired parietal with a smooth surface and a straight ,high lateral border. On the ventral side posteriorly, a median sulcus exists for the attachment of a supraoccipital process. Ahead of this groove an opening directed backwards lies on a slight elevation.

2) Ossa frontalia

The numerous frontals of the Guimarota material are represented as paired elements. The specimen Gui. GE. 3 is the only fused os frontale; it is very long and offers lateral ridges for the dorsal bordering of the orbits; the dorsal surface is grained. The paired disposition can be seen distinctly. The half frontal Gui. L. 104 presumably belongs to a related form of Gui. GE. 3.
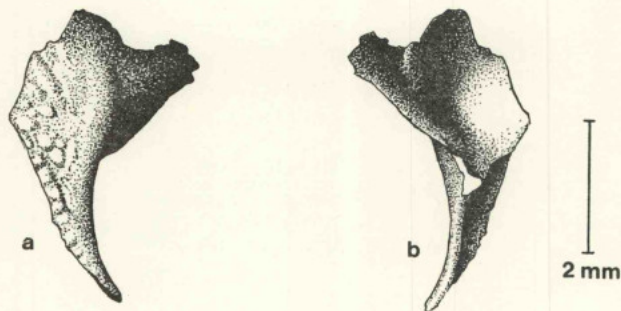

Fig. 35 — Gui. 157, right prefrontal; a: dorsal view, surface granularly patterned; b: ventral view.

Most of the frontalia fragments have a grained surface and ventrally a short, broad, lateral process in the anterior part (s. Gui. L. 36), which is medially directed (after HAAS, 1936: for enclosing the telencephalon). The posterior ends are concave in formation in order to connect with the anteriorly rounded parietal.

Some specimens are very long (Gui. GE. 30) and also reveal a long lateral ridge extending ventrally, which anteriorly turns to the descending process. Different frontalia fragments also present a long lateral ridge, but which forms medially a concave curve (Gui. 171, Gui. L. 111).

The specimens of Gui. L. 235 are made remarkable by a transversal groove (in front convex) on the dorsal posterior part of the frontal, like *Lacerta lepida*. From this groove the posterior frontal part broadens out to the the parietal. Apart from the Lacertidae these square formations also appear on Cordylidae (incl. Gerrhosauridae)

Fig. 1 — Gui. L. 139, *Macellodus* cf. *brodiei* OWEN, 1854 (cf. OWEN, 1861, pl. 8), lingual view of a tooth (stereo-scan-photo).

Fig. 2 — Gui. L. 138, *Macellodus* cf. *brodiei* OWEN, 1854, lingual view of an abrased tooth (stereo-scan-photo).

Fig. 3 — Gui. 380, lingual view of a tooth of *Cteniogenys reedi* (stereo-scan-photo).

Fig. 4 — Gui. 18, lingual view of a tooth of *Lisboasaurus mitracostatus* (stereo--scan-photo).

Fig. 5 — Gui. A. 41, tooth from the posterior part of a left dentary of *Becklesisaurus hoffstetteri*, lingual view (stereo-scan-photo).

Fig. 6 — Gui. A. 73, *Introrsisaurus pollicidens;* left: labial view of a tooth, with contact face of the base for the pleurodont attachment at the dentary; right: lingual view, tooth recurved inwards with a median elevation.

PLATES

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For the present the records are preserved under the named notations in the Guimarota-collection of the Institut für Paläontologie, Freie Universität Berlin. A later transfer into the collection of the Serviços Geológicos de Portugal, Lisboa, is intended; the type specimens of the other Guimarota faunas are scheduled for the same institution.

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The osteodermal squamation sometimes impresses its pattern to the skull bones and gives them a characteristic relief, as to be seen in some maxillae (Gui. L. 34), prefrontals (Gui. 157), frontals (Gui. L. 235) and parietals (Gui. 170) (Pl. II, 1).

K. Summary

By the management of Prof. Dr. S. HENKEL and Prof. Dr. W. G. KÜHNE, Institut für Paläontologie, Freie Universität Berlin, the little coal-mine Guimarota at Leiria (Central Portugal) yielded a rich vertebrate fauna consisting of Mammalia and abundant skeletal elements of fishes, amphibians and reptiles. The lacertilians are described with regard to the important indication of terrestrial synecologic life with the Upper Jurassic mammals. Certain findings from the localities Porto das Barcas and Porto Pinheiro have been recognised.

Skeletal elements	Anatomic number	Yielded number from Guimarota	Ratio — individuals
Jaw bones (excl. articular)	4	520	130
Articular	2	46	23
Quadrate	2	45	22,5
Squamosal	2	7	3,5
Pterygoid	2	53	26,5
Basi-occipital	1	2	2
Supra-occipital	1	1	1
Parietal	1	48	48
Frontal	2	160	80
Prefrontal	2	2	1
Nasal	2	2	1
Jugal	2	30	15
Presacral vertebrae ca.	26	232	9
Scapulo-coracoid	2	3	1,5
Clavicle	2	1	0,5
Sternal apparatus	1	1	1
Humerus	2	48	24
Radius	2	4	2
Ulna	2	7	3,5
Acetabulum	2	38	19
Femur	2	13	6,5
Tibia	2	5	2,5
Fibula	2	2	1

The ratio of the mandibles to the maxillae is 4,5 : 1.

The Lacertilia of the Guimarota are recorded by cranial and post-cranial bones often fragmented. Nine species are represented, partially very numerous specimens of certain types.

The lacertilian fauna of the Portuguese Kimmeridgian is composed of three systematic groups: Eolacertilia, Scincomorpha, Anguimorpha. The anguimorphian taxa are the rarest component. The plenty of eolacertimorphian dentaries from the Guimarota-coal refers to the phylogenetic connection with the Upper Triassic Kuehneosauridae. The family Cteniogenyidae is proposed for non-specialized Eolacertilia. The Scincomorpha demonstrate different types: there are species with modified teeth, with beginning reduction of the extremities and with the development of a vertebral zygosphene-zygantrum articulation.

of the reptiles are equally formed and the pieces have been yielded as isolated bones, it is impossible to prove that they belongto the lacertilians. Based on the proportions, the bone colour and the conic shape of the longer phalanges (typical for the lacertilians), the pieces Gui. L. 223 and Gui. L. 224 can be supposed to belong to the Guimarota lizards.

Already described by BROILI (1926) and KÜHNE (1956), the phalanges distales of the tetrapod lacertilians have a robust and thick proximal part, which is not so long in the lizards as in *Oligokyphus*. The terminal phalanges (Gui. 159, Gui. L. 227 and Gui. L. 228) can be compared with those of *Lacerta lepida, Varanus* sp. and even *Chalcides chalcides*. The dorsal articulary process for the insertion of the extensor of the terminal phalange, stretching proximalwards, and the robust ventral apophysis are correlated with the vigorous flexion of the claw (Gui. L. 159). This corresponds with the motion of strong treading (stalking after BROILI, 1926), which is deduced from the osteology of the proximal extremity. The trivial asymmetries of the terminal phalanges refer to the position in the different lateral links. The claw-bearing phalangesges distales are curved downwards and terminally tapered. On the plantar side between the saddle joint and the flexor apophysis, there is an opening (foramen nutricium). The lateral sides are distally flattened. The presented terminal phalanges probably belong to different taxa.

6) The bony tissue

The histological study of some hollow bones (Gui. L. 229, Gui. L. 215) from the Guimarota material reveals the presence of numerous cavities of the osteocytes in the bone. The lumen of the cells is relatively large, slitlike or oval, and shows dendritic processes. The osteocytes also appear in the peripheral region of the bone in the cortex. A HAVERS's system could not be stated. The same observations were made with the ulna of *Lacerta lepida* (juvenile individual) and the femur of *Chalcides chalcides*.

J. The dermal ossifications

The name Squamata for the Lacertilia and Ophidia (Serpentes) refers to their scaly skin. Above all a dermal ossification appears in the Scincomorpha and Anguimorpha, which even closes secondarily the superior temporal fenestra in the skull of many Scincomorpha (Xantusiidae, Lacertidae and Cordylidae, incl. Gerrhosauridae). Most of the Scincomorpha have composed osteoderms, in the Anguimorpha the dermal ossification produces simple bony scales (HOFFSTETTER, 1962).

In the Guimarota material numerous composed osteoderms have been found, which probably belong to the described scincomorph taxa. It is remarkable that no scale offers the distinct, smooth border for imbrication as described by HOFFSTETTER (1967) of the osteoscutes, which are assumed to belong to the scincomorph «Paramacellodus oweni». But these osteoscutes of Swanage are obviously simply formed and can rather be ascribed to the anguimorph *Dorsetisaurus*.

Several osteoderms of the Guimarota lacertilians reveal a surface which is rooflike angled, compared to it, the inner side is smooth and scarcely concave. These scales have certainly been components of the squamation at the lateral flanks of the animal, as the osteoderms of *Cordylus cordylus* are equally formed in this region. Some osteoderms seem to have a square shape (Gui. L. 37). The specimen Gui. L. 241 is the only osteoderm which indicates the imbrication of the osteoderms with the development of a special border.

The proximal part and the medial diaphysis of a tibia (Gui. L. 207) probably belong to the taxonomic relationship of Gui. L. 90. The two areas for the trochlea femoris are not distinguishable at the proximal end of the fragment Gui. L. 207. But this specimen shows a broad depression in the anterodorsal side, which has probably been referred to as the M. tibialis anticus (WETTSTEIN, 1931). Marginally near it, a bony crest is developed, which can be homologized with the cnemial crest (ROMER, 1956) of the ancestral reptiles. This marginal apophysis distinctly appears in the recent Scincomorpha. It can be referred to as the insertion of the M. extensor quadriceps femoris. The ventral enlargement has seved as the insertion of the M. pubo-ischiotibialis.

The proximal fragments of the fibula are rod-shaped and show a nearly circular articulary area, which laterally rises to a weak, proximal apex capitis fibulae, for the articulation with the femur. The contact area with the tibia is recognizable. The smaller element of the two proximal fragments differs by the presence of a ridge for the origin of the M. flexor primordialis communis (after WETTSTEIN, 1931) and by the colour of the bone. This piece belongs to the left side of the body, the second proximal fibular end to the right side.

The distal fibular ends (Gui. L. 216) are characteristically enlarged to the tarsal joint and have a triangular side. The broader articulary part is medially directed towards the tibia. A lateral malleolus posterior is lacking. The smaller piece belongs to a right fibula, the bigger one presumably to a left fibula, which has a marginal apophysis. This apophysis has probably developed for the insertion of the caput femorale of the M. triceps surae. The distal fibular end can easily be mistaken for the proximal end of the metatarsale II. The specimens Gui. 95, Gui. 176, Gui. L. 210 and Gui. L. 217 can be regarded as fragments of fibulae, which have broken ends.

4) Tarsus and metatarsus

It the present Guimarota material no tarsal element is represented. Because the tarsus (the astragalo-fibulare, the os cuboideum and an adjacent second, smaller os tarsale) can be coherently isolated by maceration in the lab, it has to be assumed, that in the natural disintegration post-mortem the terminal links of the tarsus are lost in a like manner.

The piece Gui. L. 191 probably is a left os metatarsale V. In the lacertilians the metatarsale V is proximally angled to the tarsus with a flat process, because the bone is fused in the course of development with a fibular os tarsale; it is the shortest metatarsal bone. On the proximal plantar side of the piece Gui. L. 191, the M. abductor digiti V (after SCHAEFFER, 1941) has formed a depression and a crest for the insertion. The apophysis, situated at the interior edge (processus hamatus after SCHAEFFER, 1941) for the insertion of the caput fibulare (femorale) of the M. triceps surae, is fragmentary. The opposed, dorsal side is weakly concavely curved and offers foramina nutricia and muscle marks of the extensors.

From the Guimarota, several isolated fragments of metacarpalia resp. metatarsalia are present (Gui. L. 222). The nearly symmetrical ends can be attributed to the corresponding bone of the digitus IV in the anterior or posterior extremity.

5) The phalanges

Because completely preserved lacertilian skeletons have so far not been found in the Guimarota, a form of the phalanges cannot be stated. There are present isolated pieces: relatively long phalanges proximales (Gui. L. 224), ph. mediales (Gui. L. 225) and short, robust ph. mediales distales (Gui. L. 226). Because the phalanges

the presumed strong dorsal retraction of the posterior extremity, are for the purpose of a form of motion, as described for the forelimb (cf. the chapter on the humerus).

The remains Gui. L. 30 show a swall rod-shaped femur, which indicates the presence of a lacertilian with the beginning of a reduction of the extremities.

The specimen Gui. 193 represents a relatively big left femur with a trochlea femoris, which resembles that of *Varanus* sp. and *Saniwa ensidens*. The fibular articulary part is fragmentary. This bone presumably belongs to a varanoid taxon. The right femur Gui. 16 and the left one Gui. L. 71 are relatively long bones with only a short trochanter internus. A linea aspera is not developed. Together with the specimen Gui. 193, they can be presumed to be related to the Varanoidea.

3) Tibia and fibula

The crus of the lacertilians consists of the robust anteroventral tibia and the long slender, posterodorsal fibula. Both bones stand together with their ends, they are proximally connected by articulation. The two medial diaphyses are separated by the so-called spatium interosseum.
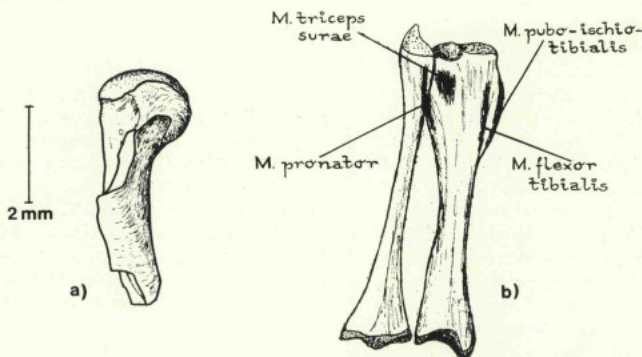
Fig. 61 — a) Gui. L. 199, proximal part of a fragmentary femur, the trochanter medius has been broken off; b) skeleton sketch of tibia and fibula of a tetrapod scincomorph lizard, flexor side.

The well preserved left tibia Gui. L. 90 (of 53 mm length) anteroventrally offers a proximal crest for the insertion of the M. pubo-ischiotibialis and distally of it, a second, medial apophysis for the insertion of the M. flexor tibialis (cf. SEIFFERT, 1970). On the opposite, fibular side of the tibia, a small articulation for the caput fibulae exists. Distally the depression in the bone indicate the origin and the pull effect of the M. triceps surae. The bipartition of the tibial articulary area for the trochlea femoris is suggested. The distal end is curved inwards; that supposes a saddle-shaped tarsal joint. The malleolus anterior has presumably been present; in this region, the distal end of the tibia has been broken. With the development of the apophyseal and articulary peculiarities, the tibia Gui. L. 90 is similar to that of *Lacerta lepida*.

The hollow bone Gui. L. 208 has fragmentary ends, but shows a distinct trunk--shaped, concave distal end. Probably this bone is the left tibia of a lizard; the fibular side of the tibia, fixed in palavit, is exposed.

more proximally than the femoro-tibial one (s. WETTSTEIN, 1931). The very small patella of the lizards has developed into the tendon of the M. quadriceps.

The right femur (Gui. L. 120) offers a well developed, but fragmentary trochanter internus and shows distally of it a linear tuberosity (linea aspera) of the bone. Further more a distinct fossa intertrochanterica posterior is developed. The condylus tibialis is latero-ventrally rendered prominent. The second specimen Gui. L. 209 corresponds with the habitus of the femur Gui. L. 120. At the going over of the trochanter internus to the distal femur shaft, there is a tubercle-like thickening, which can be correlated with the insertion of the adductors. The Mm. caudofemoralis and pubo-ischiotrochantericus function as the main adductor (after WETTSTEIN, 1931). The M. caudo- femoralis (= retractor dorsalis) of *Sphenodon* originates from the proximal ends of the haemapophyses of the first 8-9 caudal vertebrae. The muscle inserts with a thick terminal tendon distally of the trochanter internus. «Knapp vor diesem Ansatz sendet der Muskel einen schmalen Sehnenstrang distalwärts, der längs des Femurs verläuft und an der lateralen Seite des Epicondylus fibularis femoris inseriert» (WETTSTEIN, 1931). This muscle effects both an adduction and a rotation of the femur (dorsal retraction). As a profound, autochthonous pelvic muscle, the M. pubo-ischiotrochantericus (= M. obturator externus) runs from the ventral region of the pelvis to the trochanter internus, on which the muscle inserts on, proximally of the M. caudofemoralis. The M. obturator externus functions as a vigorous adductor (s. WETTSTEIN, 1931).

The M. caudo-iliofemoralis (M. piriformis after some authors) is the important auxiliary muscle of the M. caudofemoralis. The muscle originates completely from the ilium (as in the chameleon), or only partly and then additionally on the transverse processes of both sacral and the first caudal vertebrae. After the presentation of RIBBING (1938), the M. caudo-iliofemoralis of the Gekkonidae *(Uromastix)* seems to originate from some sacral and caudal vertebrae. In *Sphenodon* this muscle originates only from both sacral vertebrae. The insertion is as variable as the origin. The M. caudo- -iliofemoralis mostly inserts on the femur together with the M. caudofemoralis, which can have grown together with it. That is the posterior facies femoris in *Sphenodon*, where the inserts muscle by a tendon distally next to the trochanter internus. Sometimes the muscle also grows together with the M. retractor ventralis, which secondarily originates dorsally of the M. caudofemoralis from some anterior caudal vertebrae and runs to the ligamentum ilio-ischiadicum. This is obviously correlated with the migration of the M. retractor ventralis dorsalwards in the course of development; in *Heloderma* a muscle originates from the ligamentum ilio-ischiadicum and unites with another muscle, originating from a caudal vertebra, to the so-called M. piriformis (RIBBING, 1938). Hence it follows that the distal tubercle-like thickening at the trochanter internus in the specimen Gui. L. 109 has been caused by one of the noticed addutors. The M. caudo-iliofemoralis can be assumed as such, which is situated between the two main adductors. Such a tubercle at the trochanter internus has only been proved in the Scincomorpha *(Lacerta, Scincus, Chalcides)*.

The above described conditions are also found in four proximal femur fragments (Gui. L. 199). On these remains a further, distincter tubercle is present, which appears on the anterior facies of the femur between the caput femoris and the trochanter internus. Probably this spheric apophysis has to be referred to the insertion of the tendon of the M. caudofemoralis (retractor dorsalis). This is obviously the so-called trochanter anterior, observed in the Lacertidae and Agamidae by SIEBENROCK (1894, 1895). It also exists in *Chalcides*. Proximally of this tubercle, a foramen nutricium is present below the caput femoris. The four femora Gui. L. 199 seem to be very slender and laterally flattened in their proximal part. The piece Gui. L. 218 can be attributed to these forms. The morphological peculiarities of these femora, correlated with

NAUCK (1938) states that the spina iliaca of lacertilians is prominent by an ilium, which is distinctly curved caudally with the position of the acetabulum near the vertebral column, «was für die Übertragung der Gliedmaßenstöße auf den Rumpf und für die Ausbildung der Symphyse bedeutsam wird». WETTSTEIN (1931) also reflects upon these conditions (he gives the complementary angles) and deducts the mode of heavy motion of *Sphenodon*.

Because of the distinct spina iliaca and the recurved pars iliaca, the specimens Gui. L. 60 and Gui. L. 95 can be attributed to a tetrapod anguimorph taxon, the presence of which in the Guimarota is evident by other bony elements.

Most of the other pelvic bones offer the at first straight and then ca. 45° inclined ilia, directed dorsalwards; they probably belong to the scincomorph taxa (s. Gui. 169, Gui. L. 80, Gui. L. 85, Gui. L. 212). It is possible that some fragment (Gui. L. 144, Gui. L. 211) are to be referred to eolacertiform specimens.

The pelvic bones of the Lacertilia s. l. presumably develop from the plate elements in forms — as in the Triassic *Macrocnemus bassanii* NOPCSA, 1930 (s. PEYER, 1937), *Tanystropheus longobardicus* (BASSANI, 1886) and in the Claraziidae — to the strap-like decomposition in the recent tetrapod lacertilians and the reduction in the limbless Squamata. The aquatic *Askeptosaurus italicus* NOPCSA, 1925 (s. KUHN-SCHNYDER, 1952) from the Triassic has been specialized as «early» referring to this.

2) Femur

The caput femoris of the lacertilians is characteristically curved, corresponding with the oval forms of the acetabulum; the curvature is in vivo directed forward. The femur is connected by a capsule ligament with the pelvis in the socket of the joint (BRONN & HOFFMANN, 1890). A proximal crest-like bony process, which appears ventrally of the caput femoris, is a muscle apophysis, the trochanter internus (medius or tibialis). It is robustly developed and situated to the right of the more proximal caput; thereby the fossa trochanterica is reduced (ROMER, 1956). In some lizards on the postero-dorsal surface near the caput femoris, a tuber exists, which is correlated with the attachment of the M. iliofemoralis (the trochanter externus, posterior or fibularis). After SIEBENROCK (1895) and NAUCK (1938) two trochanters are present in the Agamidae and three in the Lacertidae. The two trochanters, always developed in the Lacertidae and Agamidae, are the trochanter internus and the small trochanter anterior. In contrast the trochanter anterior is lacking in the varanids, whereas a weakly developed trochanter posterior (fibularis) is present. In *Sphenodon* the fibular trochanter is lacking.

The longitudinal marks on the facies anterior femoris indicate the insertion of the M. pubo-ischiofemoralis internus; a ridge which appears sometimes (linea pectinea), which runs distally of the interior trochater, serves as the insertion of the M. adductor femoris (s. ROMER, 1956). In lepidosaurs a linea aspera as the distal continuation of the linea pectinea has not been observed until now; in the femur Gui. L. 120 it is present. In the lacertilians a fourth trochanter for the insertion of the caudofemoral musculature has not been proved. The femur of lizards with a rudimentally posterior extremity (as in *Chalcides tridactylus*), only offers certain tuberosities instead of the trochanters (BRONN & HOFFMANN, 1890).

The distal end of the femur has tw condyles, which are very differently developed. The condylus tibialis consists of two differing large articulary rolls; they are separated by an intracondylar furrow, which also extends to the distal bone shaft. Therewith two areas exist for the articulation with the tibia. The fibula articulates with a small facet on a so-called condylus fibularis, which is dorsocaudally situated on the posterior distal part of the femur. With this condition the femoro-fibular joint lies

dian, both ossa pubis form the symphysis pubica; on it, a straight tendon (ligamentum medianum pelvis) generally inserts, which originates from the symphysis of the two ossa ischii. The ligamentum can become cartilaginous or ossify as in *Varanus* sp. It borders the relatively broad foramen pubo-ischiadicum (= cordiforme) with the os pubis and os ischii. In many lizards the symphysis ischiadica is caudally elongated by the connective tissue, which can be ossified to the so-called os hypoischium or cloacae. In the gerrhosaurs the hypoischium is forked behind (s. BRONN & HOFFMAN, 1890; NAUCK, 1938).

The Guimarota material presents 22 right and 16 left pelvic fragments, of which the ilia are abundantly represented. The three elements are mostly fused. Some isolated fragments (Gui. L. 211) indicate a sutural connection.
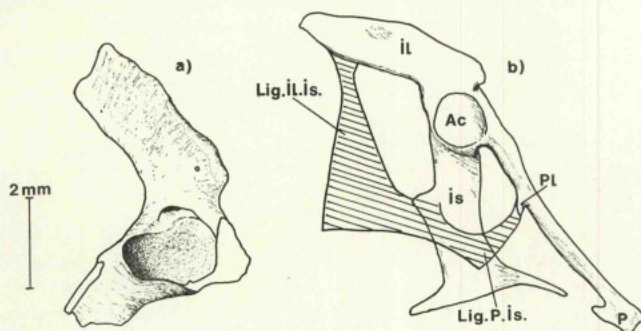
Fig. 60 — a) Gui. L. 211, pelvic fragment, right lateral view; b) pelvis of *Lacerta muralis*, right lateral view, Ac: Acetabulum; Il: Ilium; Is: Ischium; Lig. Il. Is.: Ligamentum ilio-ischiadicum; Lig. P. Is.: Ligamentum pubo-ischiadicum; P: Pubis; Pl. Processus lateralis pubis [after ROMER, 1942, p. 265].

The piece Gui. L. 60 is a left pelvis with broken ends. The pars pubica is broad and reveals a relatively large foramen obturatorium. A robust praepubic process, directed lateralwards, is present. The pars ischiadica seems also to have been broadened and caudally to have a tuber ischii. The ilium rises characteristically dorsalwards and is curved backwards.

The specimen Gui. L. 95 has a pars iliaca with a distinct spina iliaca anterior; whereas in the pelvis Gui. L. 60, this spina is only indicated by the anterior edge of the ilium. In most of the other ilia fragments the spina iliaca is scarcely distinct and can mostly be seen only on the external side (facies acetabuli) of the pars iliaca (Gui. L. 80, Gui. L. 85, Gui. L. 144, Gui. L. 211) as in the recent *Chalcides chalcides*.

The high rising shape of the ilium, which is weakly curved backwards, is also known of the pygopodids, but in these forms the pars pubica and pars ischiadica are reduced to the acetabulum (s. GASC, 1967). Because of the reduction of limbs in *Anguis fragilis*, the ventral pelvic parts are also reduced, whereas the shortened pars iliaca rises straight to the sacrum (s. HERTER, 1960). *Sphenodon punctatus* has a broad, weakly recurved ilium and a well developed ventral pelvic girdle adequate for a tetrapod form (s. WETTSTEIN, 1931).

In the agamids, varanids and tetrapod anguids, the distal pars iliaca shows an angle of 5-10° inclined to the body axis, whereas in the gekkonids the angle is 30°, in the Scincomorpha ca. 45° and in *Sphenodon* ca. 70°.

4) The carpus

The carpus of the non specialized lacertilians usually consists of nine small bones, in the proximal row: the radiale scaphoid), os centrale, ulnare (triquetrum), os pisiforme — and in the distal row: the ossa carpalia I-V. A tenth bone sometimes appears rudimentally between the radiale and ulnare, the so-called os intermedium (in *Lacerta, Tupinambis, Ameiva, Teius, Tiliqua, Eumeces, Xantusia, Gerrhonotus, Zonurus, Varanus, Heloderma*), which is always present in the Rhynchocephalia.

By the distal intercalation of the os centrale between the radiale and ulnare, both bones are always separated (BRONN & HOFFMANN, 1890; GEGENBAUR, 1898). This modification of the centrale is characteristic of the lacertilians (ROMER, 1965). From the ossa carpi of the Guimarota Lacertilia, the os centrale (Gui. L. 122) is only represented, which can be regarded as a right specimen in comparison with the carpus of *Lacerta lepida* and *Varanus* sp. The palmar side of the fossil centrale offers a foramen nutricium; this area proximally has a characteristic inclination, ending in an acute angle, because the scaphoid and triquetrum border on the centrale. Because the formation of the areas varies between the right and the left carpal bones, a taxonomic statement by the carpus is impossible.

5) The metacarpus

On a small coal piece (Gui. L. 215), a hollow bone is present, which has broken ends. It is associated with two very small, dispersed bones and fragmentary procoelous vertebrae. One of the cylindric small bones, well preserved, is axis-symmetrically formed and offers a distal articulation, which is broadened lateralwards; concluding from this feature, based on the symmetric shape, the bone can be regarded as an os metacarpale IV. The lateral enlargements for the articulation with the proximal phalange IV are distinctly developed (phalangeal saddle link; SIEBENROCK, 1894). In contrast to the nearly symmetric os metatarsale IV of the tetrapod lacertilians, the metacarpal element (Gui. L. 215) is relatively short, and proximally a little broadened. In the lizards with a start in the reduction of limbs, the conditions of the metacarpus and metatarsus are nearly similar. If the piece Gui. L. 215 belongs to a specimen of *Saurillus henkeli*, the fact cannot be exclude that the described bone is a metatarsale IV.

I. Bones of the pelvic limb

The posterior extremities are connected by the pelvic girdle with the trunk. The pelvic girdle is dorsally closed by an attachment to the sacrum.

1) The pelvic girdle

In contrast to the shoulder girdle, the pelvic apparatus develops endochondrally and ossifies in the ontogenesis. Each side has three bones, which form a socket of a joint for the femur (acetabulum). If the bones (os pubis, ischii and ilium) are co--ossified, they are termed together as os coxae and differentiated in the pars pubica, ischiadica and iliaca. The pars pubica presents the anterior ventral part, the pars ischiadica the posterior ventral one. The ilium forms the dorsal part of the pelvic girdle.

In the lacertilians the N. obturatorius always runs through a special opening (foramen obturatorium or diazonale) in the os pubis, coming from the cavum pelvicum to adductors. Cranially of the foramen obturatorium there is a small process, the tuberculum pubis or the praepubis, which is laterally directed downwards. In the me-

distal part of the ulna has a rounded condyle for the articulation with the os trique-trum (ulnare), the os lunatum (intermedium) and the os pisiforme. A processus sty-loideus ulnae is not developed.

In the Guimarota material, the radius is represented by three isolated distal ends; Gui. L. 171 concerns the distal fragments of two right radii, which show sty-loid process situated on the right lateral side in dorsal aspect, when the distal end is turned to the observer. The ventral side of these radii is flattened (as the ulnar proximal end of the radius); this flatness of one side is present in both fragments (Pl. IV, 4). The piece Gui. L. 229 probably is the distal end of a left radius.
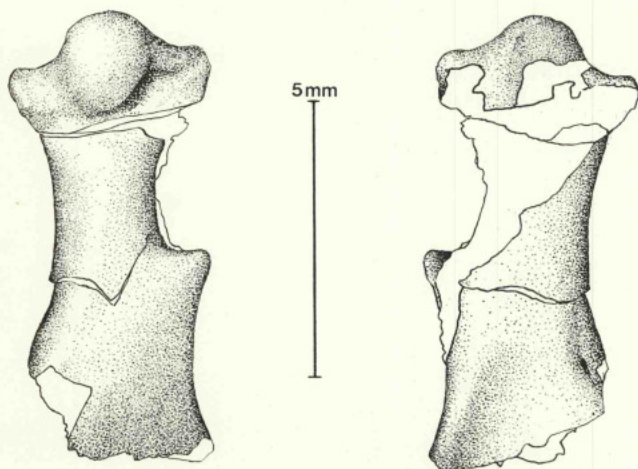
Fig. 59 — Gui. 98, fragment presumably of a right humerus, which is assumed to belong to a tetrapod with fossorial and/or arboricolous mode of life; left: posterior view; right: anterior view.

The ulna of the Guimarota lacertilians is represented by two right (Gui. L. 4) and three left (Gui. L. 205) proximal parts of this bone. In contrast to the relatively slender olecranon ulnae of *Varanus* sp., the bony olecranon of the fossil remains is very robustly developed on the outside; the tip of the olecranon is obtusely rounded. These conditions are also found in the ulna of *Lacerta lepida*. The cavitas radialis ulnae, which is at right angle to the cavitas sigmoidea, is not chiefly marginally de-veloped as in *Varanus* sp., but more towards the middle of the olecranon; at this point the articulary area is bordered by an edge. The cavitas trochlearis is a little inclined outwards. Below the olecranon, the ulna reveals a weak concavity on the outside, which passes away into the subparallel bony edges. The form of the olecranon allows the taxo-nomic statement of the found ulnae to be of non-varanoid lacertilians. This is also valid for the distal ulna fragment Gui. L. 205. On the other hand the specimen Gui. L. 221 resembles the distal end of the ulna in the varanids.

The anguid *Glyptosaurus sylvestris* MARSH, 1871 (s. GILMORE, 1928) has an equally distinct supinator crest; but in contrast to the mentioned Guimarota forms, the epicondylus ulnaris is only weakly developed with a modest broadening. The size of *Glyptosaurus* assumes the development of a crest for the extensor antebrachii radialis by function. Because in the bones of the extremities the functional differentiation is expressed, the features are not unconditional evidence of the systematic position.

Another humerus type (Gui. L. 86; Gui. L. 127 and Gui. L. 201) reveals a robust central portion, which broadens distally with a certain torsion. The proximal caput humeri is distinct, but not very broad. The tuberculum minus is weakly developed, but the deltopectoral, lateral bony crest is clearly marked. Because these fragmentary humeri are relatively small and scarcely differentiated, they could belong to lacertilians which tend to reduce their extremities (this type is represented by the scincomorph skeletal remains Gui. L. 30).

The specimens Gui. L. 81, Gui. L. 108 and Gui. L. 129 are fragments of relatively large and robust humeri. The piece Gui. L. 81 offers the dorsal presence of a long edge for the insertion of the pectoralis and deltoideus on the caput humeri; this would be typical of the Sauria. But the belonging to the Guimarota lacertilians can be presumed only, because the indicative foramen ectepicondyloideum cannot be clearly recognized (s. Gui. L. 129).

The four specimens Gui. L. 203 are in accordance with the habitus of the lacertilian humerus; the bony ends are distinctly broadened, but not rectangularly formed. A fossa supratrochlearis with an obvious foramen nutricium is present. This humerus type can be attributed to a scincomorph taxon. Probably the specimen Gui. L. 214 also belongs to this group.

The singular bone fragment Gui. 98 has been enigmatic so far, until it was compared with the humerus and femur of digging and arboricolous vertebrates, e. g. of Xenarthra *(Panochthus, Cyclopes, Myrmecophaga, Tamandua)*, of Marsupialia *(Phascolarctos)*, of Tubulidentata *(Orycteropus)* and of the badger. In these animals the anterior limb has a characteristic shape caused by the function of the shoulder musculature, especially by the M. deltoideus. The presented bone shows a remarkable process on the postero-lateral side as if it might be a right humerus. Probably this process has been developed by the insertion of the vigorous tendon of the fused deltoid musculature (pp. acromialis et scapularis), as it is known of fossorial and arboricole mammals.

3) Radius and ulna

The proximal articularly area of the saurian radius forms an oval concavity, which permits the condylus radialis (capittelum) humeri a certain rotation motility. The distal end of the radius is rather broader, flat and also oval. The characteristic processus styloideus radii reveals a crescent-shaped distal articulary area, which is adapted to articulate with the os scaphoideum (radiale); this articulation only allows a very restricted mobility.

As a special proximal formation the ulna has an elongated headed part, the olecranon. The articulary area of the olecranon articulates with the trochlear condyle of the humerus; it is termed as cavitas or incisura sigmoidea (= trochlearis). The M. triceps brachii inserts as extensor of the elbow-joint on the tip of the olecranon. In recent lizards the tendon sometimes includes a cartilaginous or bony piece, the so-called patella ulnaris (BRONN & HOFFMANN, 1890; ROMER, 1956). The main motion of the ulna to the radius is rotation inwards and outwards. Radius and ulna develop corresponding articalary areas on their proximal points of contact (incisura radialis ulnae). The

similarly and inserts as extensor of the carpus on the distal end of the ulna, on the os pisiforme and on the os metacarpale V. The muscle originates on the epicondylus radialis, which offers a distinct tuberosity (s. specimens Gui. L. 47). If a strong tramping movement of the body swinging is assumed as mode of locomotion, a strong M. flexor carpi ulnaris has to be postulated. That is conceivable for *Saniwa ensidens,* in consideration of the reconstruction of this lizard (s. GILMORE, 1928). If a broad epicondylus ulnaris is formed by function, the feature of the breadth cannot be used for taxonomic diagnosis.
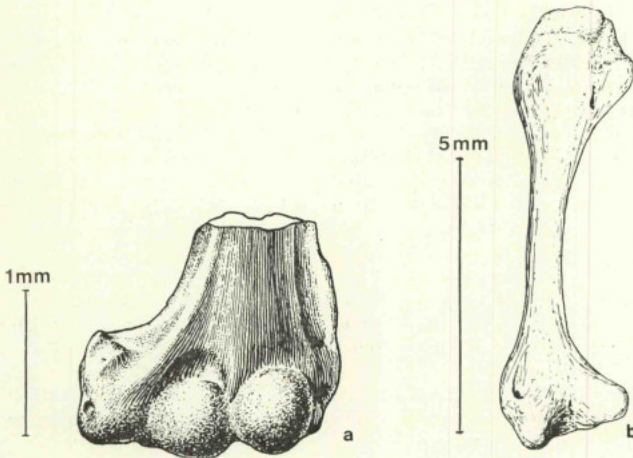
Fig. 58 — a: distal end of a left humerus (Gui. L. 145), ventral view; b: left humerus (Gui. L. 47), postero-dorsal view, with foramen ectepicondyloideum.

The distal parts of three humeri (Gui. L. 145) reveal a peculiarity. They offer a lateral, marginal crest on the epicondylus radialis; both condyles have a spheric shape, whereas the condylus radialis capitellum) is generally ellipsoidally formed in other lacertilians. A further feature of this humerus type is the prominent epicondylus ulnaris with nearly rectangular edges. The lateral distal crest of the humerus is used as the attachment for the M. extensor. antebrachii radialis and is regarded as an ancestral feature of the Lepidosauria (WETTSTEIN, 1931; ROMER, 1956). In the Eosuchia, Rhynchocephalia and Chelonia, this muscle of the forelimb is composed of three parts (M. supinator, Mm. extensor carpi radialis longus et brevis); but in the Lacertilia it is two-part or even only one-part (M. supinator + M. extensor carpi radialis caput longum et caput breve). By the contraction of this muscle, the distal anterior extremities are adduced and the carpus is extended (WETTSTEIN, 1931). The actualistic conceptions can be applied to the specimen Gui. L. 145, accordingly by the described morphological siutations of the epicondyles, an intense reciprocal action of abduction and adduction of the «forearm» can be assumed. Because after WETTSTEIN (1931) the M. supinator originates on the lateral area, the M. extensor carpi radialis on the distal area of the epicondylus radialis, the crista supinatoris of the present fragmentary humeri indicates a bipartition of the M. extensor antebrachii radialis, i. e. a prime feature. I attribute the specimens Gui. L. 145 to an eolacertiform taxon.

unimportant. In the literature by ROMER (1956) there is only found the figure of a lacertilian humerus with a fossa supratrochlearis and a foramen nutricium. In the humerus of *Varanus* sp., the fossa and the foramen are very weakly developed, but distinctly so in *Lacerta lepida*.

All the lacertilian humeri from the Guimarota mine have a foramen ectepicondyloideum and a distinct fossa supratrochlearis, the opening of which has presumably been used as the entry of a blood vessel, because there is no cavity for the passage of the N. medianus on the extensor side.

Bavarisaurus (or *Homoeosaurus*) *macrodactylus* should be reviewed as to whether the fossa supratrochlearis of the humerus reveals an opening for the canalis entepicondyloideus or not. For that purpose, the specimen is to be roentgenised or prepared after KÜHNE's method (1961) by corroding it with acetic acid; thereby the dorsal side of the humeri would be discolosed. Because the ommission of the foramen entepicondyloideum is described in the genus-diagnosis of the rhynchocephalian *Homoeosaurus*, it can not be used the comparison of homoeosaurids and lacertilians. We have to cognise that the fossa supratrochlearis is more or less distincty developed in the humerus of lepidosaurs (s. *Champsosaurus* and *Hescheleria* in PEYER, 1936; *Scincus* in EL-TOUBI, 1938; *Sauranodon* in HUENE, 1952) and that the canalis nervi mediani begins there in the Rhynchocephalia and in different other groups (s. above). In the therapsid *Oligokyphus* for instance, the foramen entepicondyloideum is not situated in the fossa supratrochlearis, but ulnarly adjacent (s. KÜHNE, 1956). Therefore we want to determine, that a foramen (entepicodyloideum) in the fossa supratrochlearis is an outlet for the N. medianus. Any other opening in this interepicondylar fossa, without a second corresponding foramen on the dorsal side of the humerus, is differently termed to prevent any mistakes.

In the lacertilian remains of Guimarota, the humeri with a specially formed distal part are abundant; their epicondylus ulnaris appears at a distinct angle to the humerus shaft, directed medialwards. In contrast to the remarkable medial broadening, the distal part of the humerus does not distinctly enlarge to the epicondylus radialis; but the epicondylus radialis is curved outwards to include the N. radialis. The N. radialis leaves the humerus on the flexor side, closely to the capitellum.

The specimen Gui. L. 47, fastened to palvit, offers the well preserved dorsal side, which has a fragmentary distal condylar part. Medially of the proximal articulary area, a well developed tuberculum minus is present for the insertion of the M. subcoracoscapularis after ROMER (1956). Below the tuberculum minus, there obviously is a foramen nutricium, which can also be observed on the same place in recent lizards. The head of the humerus has an extended, curved lateral edge for the insertion of the Mm. Pectoralis and deltoideus. The extensor of the anterior extremity has been fixed to the dorsal base of the proximal articulary enlargement. The tuberosity for the attachment of the carpal extensors is situated below the dorsal foramen nervi radialis on the epicondylus radialis; the flexors of the forelimb originate on the epicondylus ulnaris. The left humerus Gui. L. 47 represents the type which is the most numerous one in the Guimarota material (s. Gui. 181, Gui. L. 128, Gui. L. 146, Gui. L. 187). The quantity of the right and left isolated fragments is equal (14 : 14). Of the recent and fossil Varanoidea, only *Saniwa ensidens* LEIDY, 1870 has a comparable humerus with the distinctly angled detached epicondylus ulnaris. Because of the remarkable breadth of the epicondylus ulnaris, a broad insertion area for the flexors of the distal anterior extremities can be assumed. This supposition suggests itself in considering, that the M. flexor carpi ulnaris, wrich originates on the epicondylus ulnaris, is inserted on the medial side of the ulna and on the os pisiforme. This muscle abduces the «forearm» and simultaneously extends the «hand». The M. extensor carpi ulnaris functions

fimbriatus, Lacerta lepida and *Cordylus cordylus* (cf. HOFFSTETTER, 1964), the medial margin of the coracoid part shows a narrow fenestral incision. A scapulo-coracoid suture is not preserved.

2) Humerus

The lacertilians are different in the formation of the skeletal elements of the forelimb. The modifications of the skeletal parts increase in the distal direction (GEGENBAUER, 1898).

In the prime repetiles, the humerus has an oblique position to the ground and offers a torsion curvature, which brings the distal articulary areas of the humerus into a suitable position to articulate with the distal anterior extremities. As a result of the tendency to lift the body of the ground and to bring the extremities under the body to support it, the humerus becomes stretched and releases the torsion (NAUCK, 1938).

The saurian humerus is a long, unimportantly curved hollow bone, which has broadened ends. The proximal end offers two protuberances for the muscles, the tuberculum mediale (= ulnare or minus) and the larger tuberculum laterale (= radiale or maius). The lateral process is characteristically directed outwards and downwards. On the flexor side between the two processes, there is the so-called fossa intertubercularis or bicipitalis, the point of the insertion of the M. latissimus dorsi. The caput humeri is formed as a slender oblong proximal enlargement.

The condylus radialis (capitellum) and the broader condylus ulnaris (trochlea) are situated together on the broad distal end of the humerus; both radius and ulna articulate with them (BRONN & HOFFMANN, 1890; NAUCK, 1938). The long flanks of the condyles are termed the epicondylus ulnaris and epicondylus radialis (lateralis). The first one is very large and reveals a canalis nervi mediani (= entepicondyloideus) in the Cotylosauria, Mesosauria, Proganochelydia, Rhynchocephalia, Araeoscelidia, Sauropterygia, Placodontia, Pelycosauria, Therapsida and Mammalia (WETTSTEIN, 1931; NAUCK, 1938). The relatively large opening on the flexor side of the humerus (foramen entepicondyloideum) is situated in the fossa supratrochlearis (cubitalis anterior). The epicondylus radialis is only perforated in th Chelonia, Rhynchocephalia, Lacertilia s. l., Araeoscelidia, Thecodontia, Pelycosauria and rudimentarily in the Australian bird *Casuarius* (s. WETTSTEIN, 1931). Both channels are only present in the Rhynchocephalia, Araeoscelidia and Edaphosauria (Pelycosauria); they appear together with a distal broadening of the humerus. A fossa olecrani is lacking in the ancestral reptiles and the lacertilians.

A foramen entepicondyloideum is described of *Bavarisaurus macrodactylus* (WAGNER, 1852) (s. COCUDE-MICHEL, 1963; HOFFSTETTER, 1964). COCUDE-MICHEL (1963) states the foramen entepicondyloideum in a figure of the humerus of *Bavarisaurus,* but describes in the text: «Le foramen ectépicondylien est seul présent». Further the concerned figure offers a completely preserved distal end of the right humerus, although WAGNER (1852) and MEYER (1860) have already noted an outbreak in the epicondylus ulnaris dexter. HOFFSTTETER (1964) has also recognised these two mistakes made by COCUDE-MICHEL (1963). After HOFFSTETTER on the contrary the distal part of the left humerus of *Bavarisaurus macrodactylus* is completely preserved; there only exists a small pit (obviously a foramen nutricium) in the flexor side of the epicondylus ulnaris sinister. A foramen ectepicondyloideum should also be lacking as HOFFSTETTER's plates of *Bavarisaurus* show. The presence of a distinct fossa supratrochlearis is important, which has been seen by COCUDE-MICHEL (1963) and by HOFFSTETTER (1964). In recent lizards the fossa supratrochlearis is associated with a vessel-opening, directed proximalwards. Its presence has either not been noticed until now or been taken to be

the perforation of the bone corresponds with a permanent muscle action, while in the contraction a tuberosity or an apophysis projects on the humerus by the muscle pull and a regression of the bone is caused on the clavicle by the pressure of the muscle. After CAMP (1923) the further development of the deltoid muscle produces the reduction of the clavicle, at first hook-like, and finally a road-shaped form.

The clavicle of the Anguimorpha is generally simply rod-shaped; the bone is only lacking in the dolichosaurids and many mosasaurids. The iguanids usually have a long and simply formed clavicle, whereas in the chamaeleonids the bone is completely reduced in common with the interclavicle. All tetrapod and many limbless Scincomorpha have a broadened clavicle, which can be perforated or hook-like, too. In the scincids, cordylids and gerrhosaurids, this bony element is unusually broad and generally perforated (CAMP, 1923).

The dermal elements of the shoulder girdle of the «lower tetrapods» are the paired cleithra and clavicles, as the medial interclavicle. Because of the isolated medial position and of the slender structure, the interclavicle of the Sauria is only seldom fossilized, and therefore has not been found in the Guimarota material.
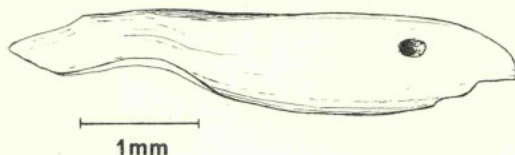
Fig. 57 — Gui. L. 198, right clavicle, medially broadened.

The specimen Gui. L. 198 is probably to be regarded as a scincomorphian right clavicle, which is medially broadened. It corresponds with the situations of Scincomorpha, described by CAMP (1923). The fossil clavicle is postmortem situated beside a badly preserved elongated sternal skeleton, which was present only as an impression. At first it was conserved by being filled with palavit and later prepared as a positive form of artificial substance. The supposed paired sternocostal elements, which are obviously located close together, can be assumed to be a parasternal development. The so-called parasternum, an abdominal continuation of the real sternal apparatus, is typical of arboricolous, as of burrowing lacertilians (s. SIEBENROCK, 1895; CAMP, 1923).

After HOFFSTETTER (1964) most recent lacertilians have a co-ossified scapulo-coracoid. The suture between both parts persists in the Agamidae, Chamaeleonidae, Varanidae, Helodermatidae, Dolichosauridae, Aigialosauridae and Mosasauridae. It is also present in the juvenile Teiidae and Anguidae, as in the skink *Riopa fernandi*. The independence and imperforation of the scapula and the coracoid are to be considered as primary conditions.

The specimen Gui. 188 is a right fragmentary scapula, which resembles that of a recent *Varanus* sp. This scapula is short and does not show any lateral fenestration, as may be seen in most known lizards. Beside small foramina nutricia situated in the marginal area, a bigger scapular opening is present in the superior part of the scapula, directed medially.The scapulo-coracoid suture is straight. Because of the similar proportions, the described scapula probably belongs to a varanoid taxon.

The scapulo-coracoid fragment Gui. L. 206 reveals two distinct fenestrations; in the superior part it exists as a large scapulo-coracoid fenestration as in the lizards *Draco*

H. Bones of the thoracic limb

The forelimbs are connected to the trunk, articulating by a pectoral-shoulder-
-girdle.

1) The shoulder girdle

Both cartilaginously created and dermal bony elements take part in forming the
shoulder girdle. The dermal covering bone, situated on the cranial side of the scapula
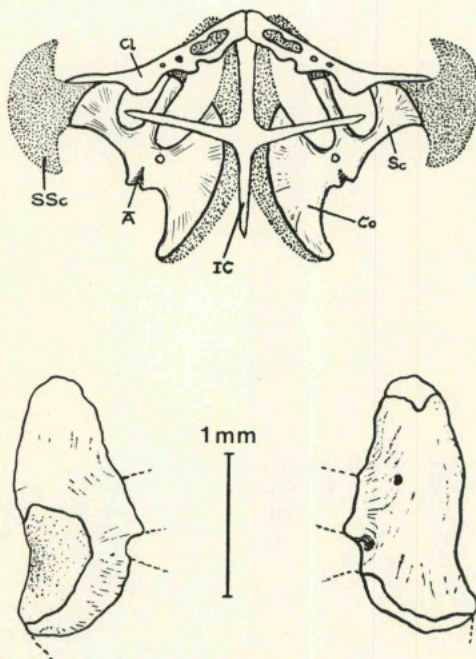in the Stegocephalia, Anura, Pelycosauria, the cleithrum, is lacking in the lepidosaurs.

Fig. 56 — Above: shoulder girdle of *Scincus scincus* [after EL-TOUBI, 1938, p. 30].
A: articulation for the humerus; Cl: clavicle; Co: coracoid; IC: interclavicle; Sc: sca-
pula; SSc: surscapular cartilage. Below: scapulo-coracoid fragment (Gui. L. 206)
from the Guimarota material, left — ventral view, right — dorsal view.

ROMER (1956) presumes that the clavicle of the ancestral Squamata is rod-shaped,
whereas CAMP (1923) supposes that the rod-shaped clavicle of saurians is derived from
a medially broadened form. Many Gekkota and Scincomorpha have clavicles broadened
towards the middle, which sometimes are perforated. The broad area of the clavicle corres-
ponds with the development of an attachment field for the musculus deltoideus (CAMP,
1923; ROMER, 1956). In the case of a nearly rod-shaped clavicle in the Gekkonidae, Xan-
tusiidae, Scincidae and Lacertidae, the bone shows distinct features of a prime breadth
and perforation. Because the deltoid muscle originates on the interior side of the clavicle,

The ribs are diversely long, the first and last ribs are the shortest. They run obliquely and ventralwards directed, whereby they show a curvature of areas and edges and a torsion. The first ribs are short and also more strongly curved than the following ones. The Guimarota material includes proximal and distal costal fragments. A prime composition of three or of two parts can not be detected. Nearly spheric costal heads are found which are distinct from the other costal bone because of a slight torsion (Gui. 199). Beside the circular articulary facts, the proximal costal fragments offer three bony ridges; the ribs seem only to be smooth, resp. without muscle insertions on the posteroventral side. The distinct ridges of the ribs indicate a bulky intercostal and levator costae musculature. In contrast all the other costal fragments have less or undeveloped ridges for the muscle insertion. Some proximal pieces (Gui. L. 195) have an oval articulary area, which is dorsoventrally broadened, and a bony crest on the anterior side.

Because the intercostal vessels and nerves run on the interior surface of the rib, sometimes a flat groove (sulcus costae) is developed; an opening for a nutritive vessel is also situated on this side. The arteria subclavia forms a very distinctive groove in the first sternal rib, providing the shoulder girdle and the anterior limbs. Because of the deep sulci costales, the specimens Gui. L. 79 can be regarded as ribs within reach of the arteria subclavia. They presumably oblong to a taxonomic costal type, which is rather smooth and rounded (Gui. 70, Gui. 78, Gui. 177, Gui. 187, Gui. L. 21, Gui. L. 78) and offers muscle insertions on the proximal part of the rib. A form with a circular articularly facet (Gui. L. 78) can be separated from a form with an oval one (Gui. 163). Six distal costal fragments (Gui. L. 196) are probably to be referred to the sternal or parasternal region because of their spheric cartilaginous ends.

Remains of associated elements of the vertebral column (cervical-lumbar), yielded by splitting the Guimarota coal, reveal smooth unicipital ribs with a circular caput costae, which is marked out by a torsion-curvature. Apart from an unimportant apophyseal development in the proximal part of the rib, no bony crests are present in these ribs.

The above named skeletal remains Gui. L. 30 indicate by a relatively short femur a beginning in the reduction of the posterior limbs (the anterior extremities are not preserved). The length of the femur (Gui. L. 30) is equal to the length of three thoracic vertebrae, whereas the one of the femur of *Lacerta lepida* corresponds to the fourfold, and of *Varanus* sp. to the fivefold length of a thoracic vertebra. The thoracic vertebrae of the skeletal remains are not elongated, but proportioned as in *Lacerta lepida* with a zygosphene-zygantrum-development. Therefore it can be assumed, that this lacertilian form had kept moving by winding in addition to the quadrupedal locomotion, similar to the cordylid *Chamaesaura aenea*.

«Thus the vertebral column of the Squamata is best studied as an entity without focusing on a single character. Some attempts have been made to elicit patterns by means of biometrical methods, or to characterize the functional basis of the morphalogical diversity.» (HOFFSTETTER & GASC, 1969)

The specimen Gui. L. 200 resembles the special caudal vertebra of *Lacerta lepida* in particulars, which is situated immediately ahead of the caudal vertebrae with an intravertebral or autotomic septum (i. e. the seventh of Lacertidae, the fifth caudal vertebra of most other lacertilian families). In this caudal region of the vertebral column, the Lacertilia and Rhynchocephalia can cast off the posterior tail part by the so-called autotomy in distress. The procoelous vertebra Gui. L. 200 reveals large, obliquely inclined zygapophyses, further slender and straight transverse processes and a reduced spina dorsalis. By the postmortem deformation, the posterior vertebral part is a little translocated into the anterior part, in the region of the potential autotomic septum (i. e. caudally of the transverse processes). A small sagittal crest on the anterior part of the neural arch, missing on the posterior one, indicates the presence of an intravertebral septum. The posterior part of the neural arch is rounded and seems to end caudally in a small process, rising dorsalwards. Because there is no known autotomy of the Varanoidea, the described specimen belongs to a non-varanoid taxon and a non-aquatic form.

The other caudal vertebrae (Gui. 136) have very compact centra, but the vertebral arches and pleurapophyses have been broken off. The centra offer a distinct ventral median crest, which caudally seems to diverge to the haemapophyseal marks. An autotomic septum is missing. A special taxonomic determination of these fragments is impossible. The Guimarota material has yielded only two fragmentary lacertilian haemal arches (Gui. L. 170), which presumably belong to two different taxa because of the appearance and bone colour.

5) The ribs (costae)

A vertebral segment primarily has one pair of ribs. The ribs are regionally discriminated. In the reptiles they are used in respiration, and for other and additional important functions in certain skeletal regions or in the case of reduced limbs. The ribs support the body wall, and are also of use in locomotion.

After REMANE (1936) the reptilian ribs are primarily separated into two of three successively situated parts: the proximal segment is named vertebrocostale, the small intercalated piece is the intercostale and the ventral, distal segment is the sternocostale. On the posterior side of the vertebrocostale, there is often present a processus uncinatus, but which is lacking in the Squamata. The tripartition of the rib exists in the Rhynchocephalia and some Lacertilia (Agamidae, Scincomorpha).

Instead of the prime dichocephal ribs in the ancestral reptiles for the articulation with the parapophysis and the diapophysis, the lacertilians only have unicipital (syncephal, holocephal) ribs, because both vertebral apophyses are fused to the synapophysis. Functionally the proximally forked rib is to be regarded as phylogenetically primary, because the double insertion of the rib creates to stability and thus has a suporting function. A dichocephaly is only presented on the cervical ribs of the Rhynchocephalia and weakly indicated in *Varanus* sp. The sometimes oblong shape of the saurian synapophysis indicates the prime dichocephaly of the reptilian rib. In contrary to the Rhynchocephalia, the Sauria do not have any processus uncinati and any wing-shaped, broad sternocostalia.

In many cases of limblessness, a so-called processus tuberculiformis appears in the front of the coastal head, which does not bear any relation to the prime dischocephally, but is of use for the insertion of the intercostal muscles. Sometimes there even exist two small costal processes, which are anteroventral and posterodorsal of the costal facet. Their lacking, resp. their size is characteristic for the degree of the limb-reduction in Scincoidea (s. HOFFSTETTER & GASC, 1969).

Two specimens (Gui. L. 182) of different bone colour (whitish and dusky) repre-
sent the forms without zygosphene-zagantrum-development. These vertebrae are stout
and they have broad pleurapophyses. The light vertebra offers small prezygapophyses,
which are not directed inwards, and distinct marks on the centrum for the attachment
of the haemal arches. The dusky specimen has a large prezygapophysis, medialwards
directed, and attachment areas, nearly intervertebrally situated, which indicate the pre-
sence of haemal arches. The two vertebrae obviously are of the anterior caudal region.
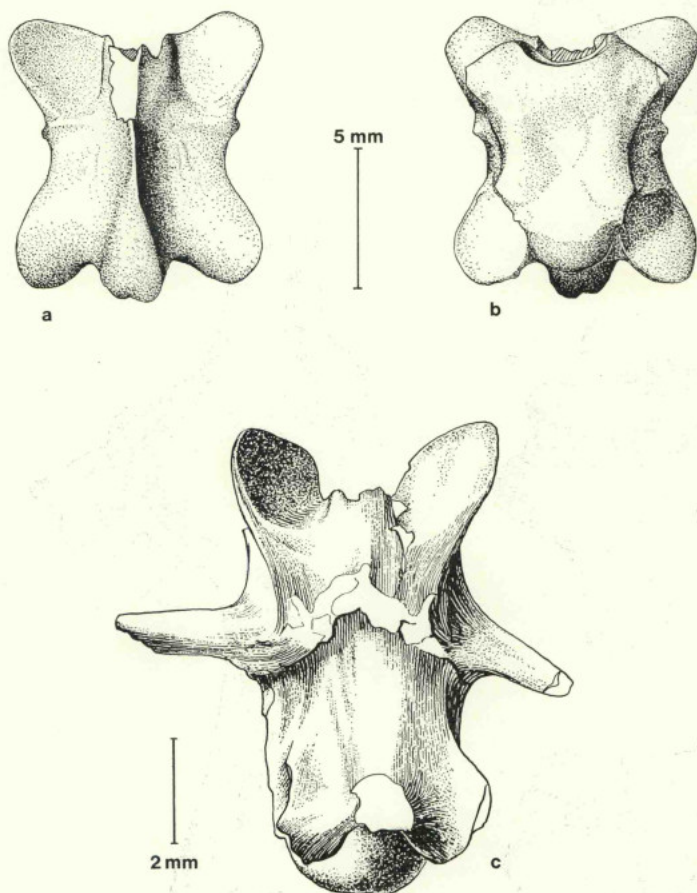
Fig. 55 — Vertebrae assumed to belong to the same lacertilian taxon (presumably
Lisboasaurus); above: thoracic vertebra (Gui. L. 1973) with morphologic peculiarity,
probably caused by the M. retrahens costarum (e. g. costal locomotion), a: dorsal view,
b: ventral view (shape similar to that of *Trachysaurus* and Anguoidea); below
(c): caudal vertebra (Gui. L. 200), dorsal view.
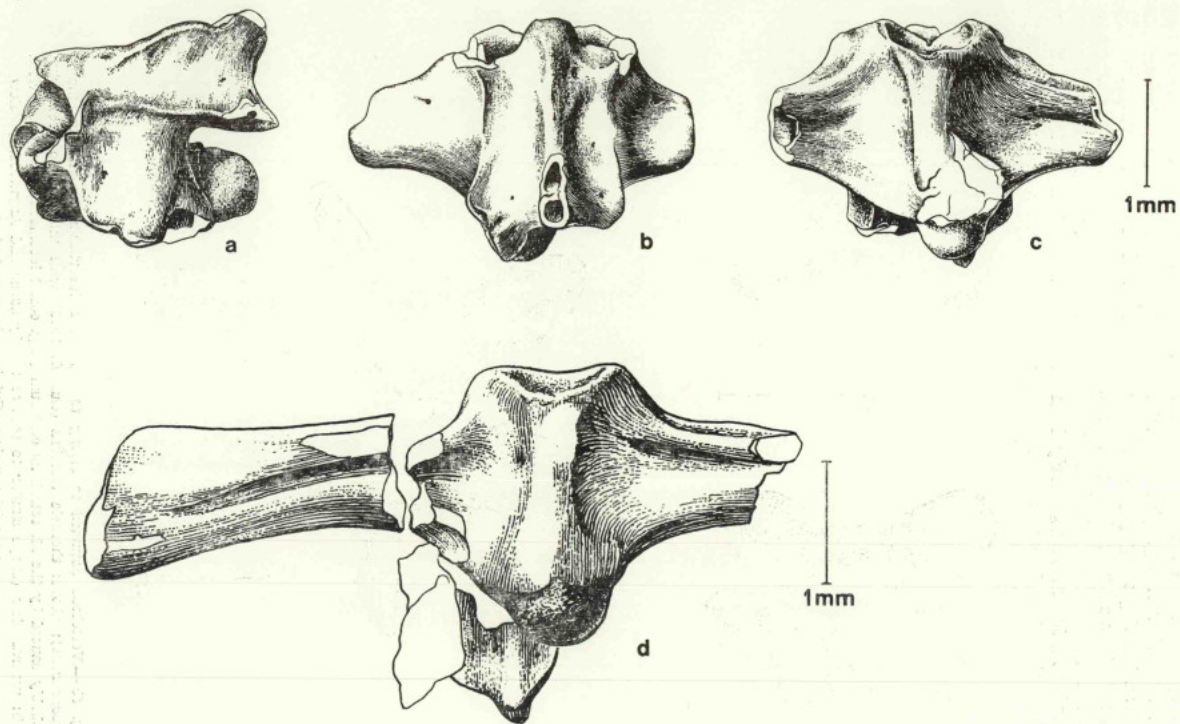
Fig. 54 — Pygal vertebrae, a-c: specimen Gui. L. 124, d: specimen Gui. L. 76; a: left lateral view, b: dorsal view, c: central view, grooving of the transverse processes is indicated; d: ventral view, distinctly grooved processus transversi.

given with a peculiarity: on the right anterior pleurapophysis, a presumable insertion mark exists as a notch for the last presacral rib, as described in the regio sacralis of the recent *Iguana* sp. after WILLISTON (s. REMANE, 1936). The distal fragmentary pleuraphyses are subcylindric and retrovert, indicating a distally larger attachment area for the ilium. The transverse processes have proximally two vessel-openings in their caudal sides. Whereas the cranial cotyle is hemispheric, the condyle seems to have an ellipsoidal form. This is obviously correlated with the breadth of the sacrum. The neural arch is slightly deformed and pressed into the neural channel. It is a little notched in the middle of the anterior part. Apparently the postzygapophyses are reduced, as an indication of a close connexion of the two sacral vertebrae (a scincomorphian habitus). There are no indications of a fusion with the second sacral vertebra.

The vertebral fragment Gui. L. 181 reveals a broad, cranially curved transverse process, which proximally has a distinct ventral foramen (for the passage of lymphatic vessels after HOFFSTETTER & GASC, 1969). Another feature is the small prezygapophysis with a zygosphene-development. In all probability the piece can be considered as a second sacral vertebra. The cranial cotyle articulates with a nearly ellipsoidal condyle.

Below the two sacral vertebrae connected with the ilia, the first vertebra already belongs to the tail region. Sometimes this vertebra can be fused with the sacrum. It has remarkably long and broad transverse processes, which usually offer a proximal ventral foramen or sometimes even a transverse channel, whereby the pleurapophyses seem to be groved on the ventral side. Further more this vertebra is characterized by the lack of ventral haemal arches, which are otherwise presented with attachment marks in the regio caudalis. The vertebra is also named pygal vertebra, because it is postsacrally and topographically situated in the collecting area of the caudal lymph, terminating in the trunk.

The vertebral specimens Gui. L. 76 and Gui. 124 bear long and broad transverse processes, which are ventrally grooved (s. palavit preparation Gui. L. 76). A zygosphene-zygantrum-articulation is developed on the apophyses of the vertebral arches. In contrast to the typic caudal vertebrae, the zygapophyseal areas of these specimens are not distinctly directed inwards, resp. outwards. The vertebral centra do not show any indication of the presence of haemal arches. This diagnosis conforms to that of a pygal vertebra. In the forms without zygosphene-zygantrum-development, any sacral- or pygal vertebra are not represented, but only posterior caudal vertebrae are found.

4) Regio caudalis

The caudal vertebrae are generally present more numerous than the prepygal vertebrae. The exceptions are correlated with the locomotion and the form of life of certain forms. In the yielded Guimarota material the caudal vertebrae are less numerous than the thoracic ones. Probably this phenomenon can be referred to the disintegration of the vertebral column by the natural, postmortem maceration, beginning in the caudal region.

The tail vertebrae are characterized by relatively long, straight transverse processes and the presence of ventral haemal arches. These arches with a paired insertion are intervertebrally situated and articulate together with two successive vertebrae. In agamids there is a tendency to shift the insertion to the posterior vertebra; in scincids, cordylids and gerrhosaurids, also some Anguimorpha (*Xenosaurus* and *Shinisaurus*), the haemal arches move to become inserted under the condyle of the preceding vertebra. In anguids, anniellids, amphisbaenids and in the snakes, the arches are fused with the centrum.

the lymphatic vessels; they also cover the lymphatic channel connecting the lymph hearts with the median perivascular lymphatic clearance. Such transverse processes are often distally forked and moreover have a proximal foramen ventrale.

The inclusion of the last presacral vertebra in the sacrum is known not only of Saurischia, but also of Iguanidae (s. REMANE, 1936). The last presacral rib (= lumbar rib) of *Iguana* sp. inserts distally in the anterior pleurapophyseal end of the first
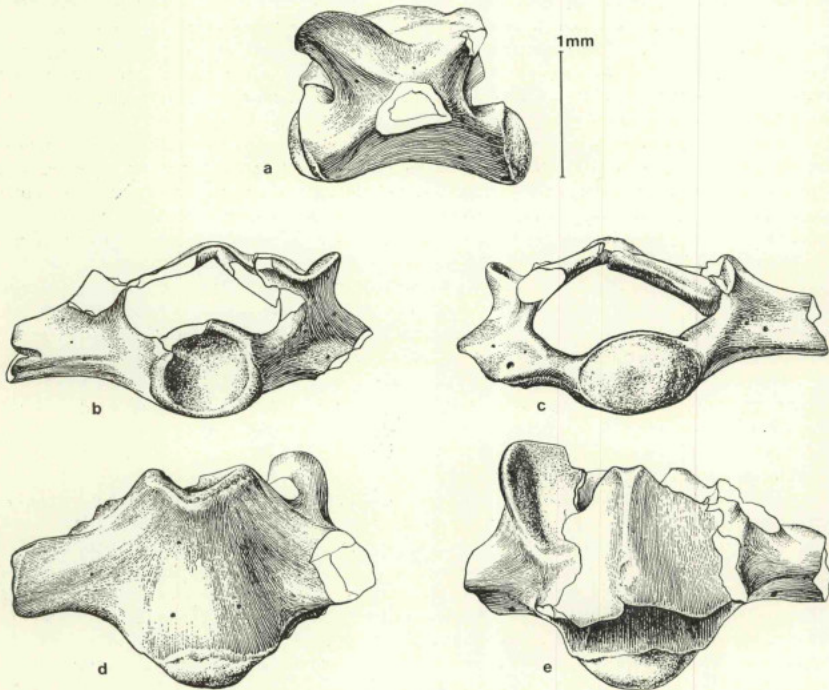

Fig. 53 — Gui. 168, sacral vertebra I; a: left lateral view; b: cranial view, distinct zygosphene formation and remarkable contact area for the last presacral rib on the right transverse process; c: caudal view; d: ventral view; e: dorsal view, zygosphene formation at the prezygapophysis.

sacral vertebra. This habitus is probably to be referred to as supporting function of the pelvis in lifting up the upper part of the body and in an arboricolous mode of life. The last presacral rib of the Anniellidae has another function in connexion with the considerable reduction of the pelvic girdle. From this lumbar rib of *Anniella* sp. connecting fibres pass to the apophyseal end of the first sacral vertebra and to the rod-shaped ilium (s. GASC, 1967).

By the stated features of the lacertilian sacral vertebrae, the specimen Gui. 168 can be determined as being a first sacral vertebra. The shape is short and stout, broad and ventrally flattened. The vertebra has remarkably large prezygaphyses with distinct zygosphene-development. Thereby a stiffening of the sacrum has been

The Guimarota material moreover comprises vertebrae and vertebral arch fragments with zygapophyses and without a zygosphene-zygantrum-forming. Most of these forms (Gui. 377, Gui. L. 18, Gui. L. 66) presumably oblong to anguimorphian taxa (cf. the diagnosis of Gui. L. 179).

A vertebral type of frail structure is remarkable (Gui. L. 134, Gui. L. 162, Gui. L. 178); the vertebra is distinguished by the partly translucent, yellow-brown bone tissue. The centrum is solid; foramina subcentralia are present; each side offers a ventrally increased articulation for the rib (s. Gui. L. 162). Therefore the corresponding rib may reveal an oblong articulary facet, which would indicate the prime double--heading of the rib. The vertebra Gui. L. 134 seems to be the last thoracic one above the pelvic girdle. The articulation areas for the ribs are lacking; the neural channel has a narrow lumen; the prezygapophyses are small, the postzygapophyses are enlarged for an articulation with the increased prezygapophyses of the first sacral vertebra. The moderate and obtuse spina dorsalis is bilaterally limited by a groove, which originates by the genuine profound dorsal musculature. In general the spina dorsalis increases caudalwards.

The specimen Gui. L. 180, determined as a lumbar vertebra, does not show any costal insertion, but offers a small, retrovert processus transversus. The centrum seems to be shortened. The prezygapophyses are very small and obliquely directed inwards in a way, which suggests the condition of opposite accessory facets. In view of the very moderate spina dorsalis, the extremely short transverse process and the missing hypapophyses, the described vertebra does not belong to thesacral or caudal region.

3) Regio sacralis

Several vertebrae (Gui. 168, Gui. L. 76, Gui. L. 124, Gui. L. 181) have special transverse processes. In the cervical and truncal vertebral column, the lacertilian vertebrae offer synapophyseal articulary headings for the insertion of ribs. Contrary to the vertebrae of the presacral region, which have short transverse processes in some groups, the sacral vertebrae bear elongated and broad transverse processes, which are also termed pleurapophyses because of their wing-shaped aspect. Free sacral ribs are lacking in the lacertilians. By the ossa ilia the pelvis is directly inserted in the first two vertebrae with pleurapophyses, which in fusion are termed os sacrum. After HOFFSTETTER & GASC (1969) the sacrum of tetrapod lizerds is formed by the 25th and 26th vertebra (in Iguanidae, Agamidae, some Lacertidae and Teiidae), in *Varanus* sp. by the 30th and 31th vertebra. Exceptionally a third vertebra functionally participates in forming the sacrum, as HOFFSTETTER & GASC (1969) have observed in *Nephrurus* sp. (Gekkonidae) and *Gerrhosaurus flavigularis* (Gerrhosauridae). Mostly the vertebral centra and arches of the two sacral vertebrae are fused, as are the ends of the pleurapophyses; an opening resists between the transverse processes (= foramen sacrale). In most of the Teiidae, Scincidae and Gerrhosauridae, the size of the sacral foramen is reduced by the close fusion of the pleurapophyses.

The first sacral vertebra is generally stronger than the second one. The pleurapophyses are subcylindric, extended and partly inclined; they form the larger part of the attachment area for the ilium. The transverse processes of the second sacral vertebra are thinner and distally forked in some forms; in this case the ilium is situated on the anterior branch.

The tendancy for limblessness influences the position and morphology of the sacrum, because the number of the presacral vertebrae increases, as the pelvis and the extremities are reduced. Thereby the function of the pleurapophyses, as a support of the ilia, is replaced by the transformation of the transverse processes for protecting

The obliteration of the sagittal crest in some vertebrae, ventrally situated, does not have any diagnostic signification. Within the thoracic vertebral column of recent Scincomorpha *(Lacerta lepida, Chalcides chalcides)*, the ventral side of the vertebrae becomes smooth, from the lumbar region to the second sacral vertebra, whereas con-
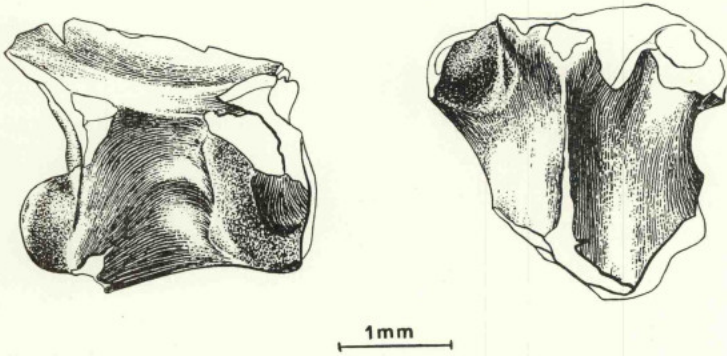

Fig. 51 — Gui. L. 162, thoracic vertebra; left: right lateral view, oblong articulary area for the rib; right: dorsal view, at the prezygapophysis the zygosphene development begins.
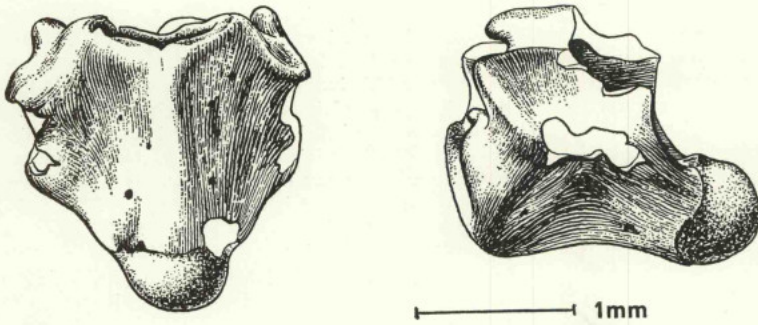
Fig. 52 — Gui. L. 180, lumbar vertebra; left: ventral view; right: left lateral view.

trary in the Anguimorpha, the ventral crest is reduced in the main part of the thoracic vertebral column and even appears again in the lumbar region.

The type of flat vertebra (Gui. L. 179), which is anteriorly broadened and ventrally smooth, reveals an anguimorphian habitus with a shortened, broad condyle and a broad, elliptic cotyle. The so-called foramina subcentralia do not have any systematic signification, as HOFFSTTETER & GASC (1969) assume for Gekkonidae and Xantusiidae. Foramina which usually appear in pairs, bilaterally of a sagittal crest, are also present in recent skinks *(Chalcides chalcides)*, lacertids *(Lacerta lepida)* and certainly in other groups. This positioning of vessel openings are found on numerous vertebrae of Guimarota.

Zonosaurus), in some lacertids and teiids, the fossil varanids *Megalania* and *Saniwa,* in the dolichosaurids and some mosasaurs (REMANE, 1936; HOFFSTETTER & GASC, 1969).

In *Sphenodon* this articulation is only suggested by an upward tendency of the prezygapophyseal facets. The specialization of the zygosphene and zygantrum in snakes, iguanids, the teiid *Tupinambis* and some mosasaurs appears with the inclination of the anterior accessory articulary areas to latero-ventral (zygosphene) and of the posterior to latero-dorsal (zygantrum), so that the area of the prezygapophysis faces that of the zygosphene, whereas those of the postzygapophysis and zygantrum are turned away mutually.
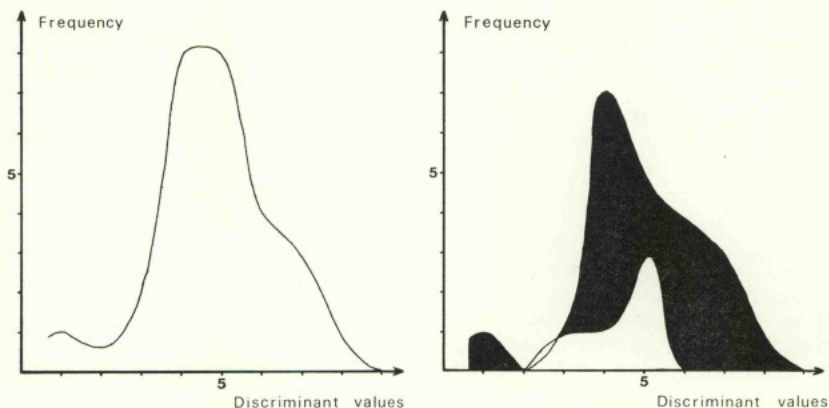
Fig. 50 — Diagram of distribution (s. text).

The zygosphene-zygantrum-articulation seems to produce a stiffening of the vertebral column by take effect of locking the torsion. Such articulation usually appears in snakelike extended forms; the presence in large forms is remarkable. Zygosphene and zygantrum offter their primary situation in the vertebrae of lacertids, cordylids, *Zonosaurus* and *Saniwa*; the described articulary areas of them are situated nearly vertically to the lightly inclined zygapophyses.

After HOFFSTTETER & GASC (1969) the zygosphenes often reveal an intracolumnar morphological variation, which stretches from a rudimentary state in the cervical region to a specialized development in the posterior truncal region; they are extinguished in the tail (e. g. *Saniwa ensidens* LEIDY, 1870). The zygosphene development is independent of a reduction of the limbs and the size of the animals.

The vertebrae of Guimarota are relatively numerous, but very fragmentary. The crocodilian vertebrae can be separated easily by their light brown, heart-wood-coloured bones. The saurian thoracic vertebrae with preserved neural arch Gui. L. 161 and Gui. L. 133 offer the well developed zygosphene-zygantrum and the described differences of the proportions in the same material. By that the systematic unity of the vertebral fragments (Gui. L. 175 and Gui. L. 176) studied with LINDER's numeric methods (1964), and of the vertebrae with the zygosphene-zygantrum-articulation (Gui. L. 161, Gui. L. 133) can be concluded. Some fragments (Gui. L. 160) have marks of an added developed articulation vertical to the zygapophyses. They are to be seen articulating vertically to the zygapophyses. They are to be regarded as related (generically or subgenerically) to the above described forms with zygosphene-zygantrum.

the centrum is determined by measuring the distance from the cotylar margin to the beginning of the condylar, the breadth is given by the distance between the two synapophyses. The discussed vertebral remains have synapophyseal articulated heads for the ribs; on the vertebral side of these vertebrae there is found no mark to suggest the presence of intercentra.

The vertebral proportions can be regarded as a function of the mode of life (e. g. the intense cotylar-condylar articulation of skinks which move on winding by reason of the reduction of limbs). Different locomotion makes specific biotops accessible. The biological and phylogenetic consequences of the selected features are appropriated in order to determine the species. But this aspect is complicated by the repeatedly apparant adaptation of the skeleton to an apod locomotion in the Squamata. Thereby after GASC (1967) a complex of features results from the modifications associated with the mode of life, from adaptive particularities and from the genetic situations, which causes one to examine the complete vertebral column. For the study of the proportional differences in the selected thoracic vertebrae, the topographic limitation meets the requirements.

The deviations of the measurement results (data of asymmetry) for the centrum-length refer to a variation within the thoracic vertebral column. By evaluating the dispersion of the differences of the mean values ($S_D = \pm 0{,}744$), the mean values ($M_{\text{Gui. L. } 175} = 4{,}951$ and $M_{\text{Gui. L. } 176} = 4{,}338$) and the t-datum ($t = 0{,}824$), the probability ($P = 0{,}47$) arises that both groups of measurements derive from the same basic entity. Just so the comparison of the difference of mean values with the threefold or even the twofold of their dispersion ($D_M < 3\text{-}2\ S_D$) shows that the difference is to be regarded as being accidental and that both groups of measurements descend from the same material. The so-called F-distribution for the statistical underpinning of a distance from zero does not allow a separation ($^3_{24}F = 4{,}99$; $F_{(p=0{,}05)} = 4{,}53$).

The distribution of the discriminant values (X) of both groups does not allow any separation. The synopsis of the distributed quantities gives the diagram of a nearly standard distribution. A light asymmetry of the distribution of the breadth-measurements is to be referred to the obvious deformation of the material (s. diagenesis and tectonics of the matrix in HELMDACH, 1968). The deviation of the measurements of the centrum-length from the standard distribution depends on the variation of the vertebral length within the vertebral column, i. e. by increasing of the length from cervically to lumbarly. With the diagram both groups of vertebrae can be accounted for vertebrae of an anterior and a posterior region of the thoracic vertebrae.

Both hypothetically separated groups of measurements show a contrary asymmetry of distribution in the right diagram (Fig. 50). The additive diagram (left) of the quantities of the discriminant values (synthesis of the two separate curves) resembles that of a GAUSS's distribution of quantities. Accordingly both measure groups belong to an uniform entity, which are falsely separated after any insignificant proportional differences within the thoracic vertebral column.

In several lacertilian families the neural arch develops to a different degree the zygosphene-zygantrum-articulation. It concerns the two additional articulary areas between the prezygapophyses and between the postzygapophyses. These accessory articulations are only present within the order Squamata; they have apparently come into existence in several groups, independently of one another (a phenomenon of convergence), and they appear in like manner on the vertebrae of tetrapod and limbless forms. This described feature is characteristic of all snakes, but it is sporadically presented in the lizards as in the large iguanids, the cordylids (not gerrhosaurs, except

cervical material seems to be rightly attributed to the Scincomorpha (with C_{1-8}). The intercentra are represented by only one specimen (Gui. L. 172).

2) Regio thoracalis

The thoracic vertebrae of the lizards generally bear ribs, the first five pairs of which are usually connected with the sternal apparatus. For coastal articulation, they have developed a reniform or spherical, cartilaginous small head below the prezygapophysis of each side.

In the lumbar region of the trunk (l. e. one to three vertebrae above the first sacral vertebrae), the ribs are sometimes missing or an ankylosis of reduced ribs and corpus vertebrale is present. In the families Scincidae, Gerrhosauridae and Lacertidae, the presacral vertebrae are never ribless (after HOFFSTETTER & GASC, 1969).

As a characteristic and convergence-development the Upper Triassic eolacertilians *Kuehneosaurus, Kuehneosuchus, Icarosaurus* on the one hand and the recent agamid *Draco* have elongated synapophyses with broadened articulary areas for the long ribs, which are allowed to glide by the extended integument (ROBINSON, 1962, 1967a; COLBERT, 1966, 1970). Thoracic vertebrae with elongated, articulary transverse processes have not been found in the lacertilian remains of Guimarota.

The saurian centra mostly show a sagittal, blunt crest on the vertebral side, which is related with the ontogenetic constriction of the chorda dorsalis. The osseous material which has replaced the reduced chorda gives the vertebral conus a hourglass-shaped relief, as already described above.

In numerous Anguimorpha and some limbless Scincomorpha, the ventral surface of the vertebra is flat and the blunt median crest is obliterated. It is possible for the condyle and centrum to have been broadened. Sometimes the lateral borders of the centrum are less divergent (Scincidae).

The reduction of the limbs is correlated with an increase of the vertebral segment number and with the tendency to an uniformity of the vertebrae. The length of the vertebrae varies in relation to the function of the mechanical conditions of the vertebral column. Apart from *Varanus* and *Lanthanotus,* the lacertilians with well developed limbs possess relatively short cervical vertebrae. The vertebral length considerably increases towards the pectoral girdle and reaches its maximum in the posterior thoracic region. In the lumbar presacral region, the vertebrae are shortened again but never so short as the cervical ones.

From a part of the Guimarota vertebral material without preserved neural arches, two different groups of vertebrae with the same habitus and certain proportions are to be collated. In one group (Gui. L. 175) the breadth of the vertebra is in the ratio of the total length of 1 : 1, and the length of the centrum to the length of the condyle of 3 : 1; whereas in the other group (Gui. L. 176) a ratio of breadth to centrum-length of 1 : 1 can be stated, and a ratio of centrum-length to that of the condyle of 4 : 1. Whether this difference is a specific feature or is related to an intracolumnar increase of the centrum-length from cervically to lumbarly, has been studied biometrically with discriminating analysis.

The biometry has supplied methods which also permit an exact review of the measurement results of a moderate quantity (s. BELITZ, 1960). The presumed differences can be computed with discriminating analysis, whereby a hypothetic separation is either statistically certain or denied.

The length and breadth of the vertebral centra and the length of the condyle are taken as features for the discriminant function. By this a deviation or a conformity in proportions within the examined groups can be evaluated. The length of

tebra; on the fifth of most Agamidae and Iguanidae and of the cordylid *Chamaesaura;* on the sixth and seventh on the Varanidae (s. HOFFSTETTER & GASC, 1969).

In all probability the best preserved specimen (Gui. L. 45) is the fourth cervical vertebra of a scincomorph lizard, considering its transverse process is characteristically formed like that of the fourth cervical of *Chalcides chalcides* and equally so like the sixth one of *Varanus* sp.; the transverse processes of the ribless cervical vertebrae offer a certain obliquity to the vertebral centrum, whereas they are nearly
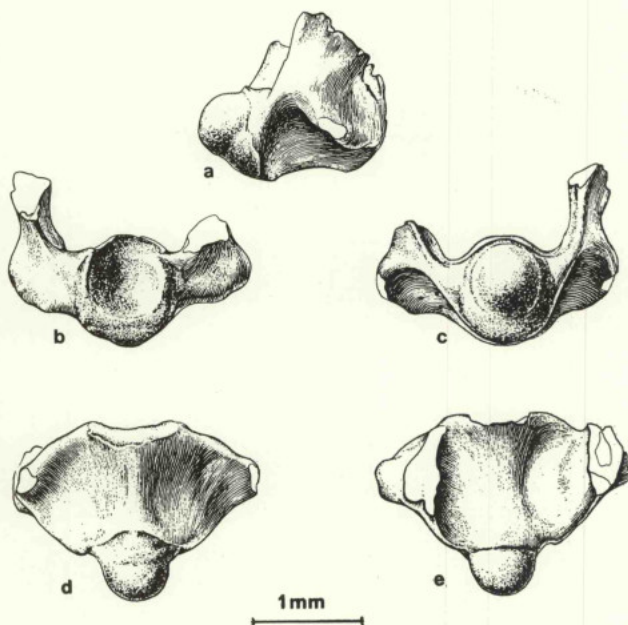
Fig. 49 — Gui. L. 45, anterior post-axial cervical vertebra (probably C.); a: right lateral view, the intervertebral position of the intercentrum can be supposed; b: cranial view; c: caudal view, the contact area for the intercentrum has been developed; d: ventral view; e: dorsal view, the neural arch has been broken off.

vertical on the rib-bearing cervical vertebrae and have also developed a roughly spheric articulary head of the rib.

The cervical vertebra connected with the first rib has a rather oblique transverse process. The distal end is formed only as a convex chondrial articulation area, not a typical articulary head. The figured specimen shows the thinning out of the substantia compacta on the costal area of the transverse process (Fig. 49).

From the other fragmentary cervical vertebrae, one part has obliquely directed synapophyses, the other part nearly spherical ones. The ratio of the delivered anterior (C_{3-5}) and posterior (C_{6-8}) cervical vertebrae is approximately equal.

After the previous aspects and because of the above described intervertebral position of the hypocentra (therefore intercentral) with the characteristic marks, the

backwards, has been developed. The odontoid process is shaped like a small, protruding lip.

In coming to a decision over the taxonomy, it may be ascertained that the intercentra are obviously set between the vertebrae, resp. on the cranial part of the following pleurocentrum (typ: Cordylidae, the young with an intervertebral intercentrum and the adult with an antero-subsequent one, s. HOFFSTETTER & GASC, 1969). As the Anguimorpha, Scincidae and Gerrhosauridae tend to reveal a hypocentrum, caudally set on the vertebra, the presented specimens are determined probably as scincomorph, cordylid-lacertid (not teiid) axial types.
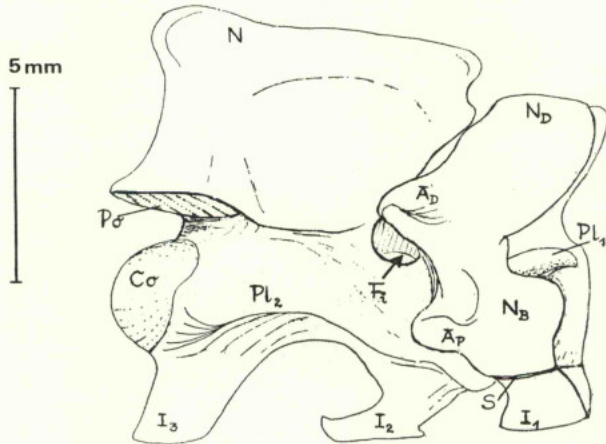
Fig. 48 — Right lateral view of the atlas and the axis of a recent varan; A_D: dorsal apophysis (diapophysis); A_P: parapophysis; Co: condyle; F_i: fenestra intervertebralis; $I_{1, 2, 3}$: intercentra; N: neural arch; N_B: base of the neural arch (pediculus arcus); N_D: tegmen of the neural channel; $Pl_{1, 2}$: pleurocentra; Po: postzygapophysis; S: synchondral joint.

b)   Post-axial cervical vertebrae:

In defining cervical vertebrae, HOFFSTETTER & GASC (1969) have soundly advised one to follow that of STANNIUS (1849). Accordingly vertebrae of the cervical region are those located cranially of the vertebra, the rib of which is first connected to the sternum. As the Guimarota material has not yielded any associations of the cervical vertebral column and the pectoral girdle, other criteria have been used to characterize cervical vertebrae.

The compactness and shortness of the vertebral centra diagnose the cervical vertebrae of Sauria as do the high-rising neural arches which enclose the thick cervical medula spinalis, and also the unpaired attachment of the hypocentrum and the habitus of the synapophyseal processes.

16 of the Guimarota vertebral fragments are thought to be post-axial lacertilian cervical vertebrae (Gui. L. 45). The first rib of most lacertilians appears on the fourth cervical vertebra, of the scincomorph genus *Dibamus* on the axis itself, of some Gekkonidae, Pygopodidae, Scincidae, Anguidae, Anniellidae and of *Xenosaurus* on the third ver-
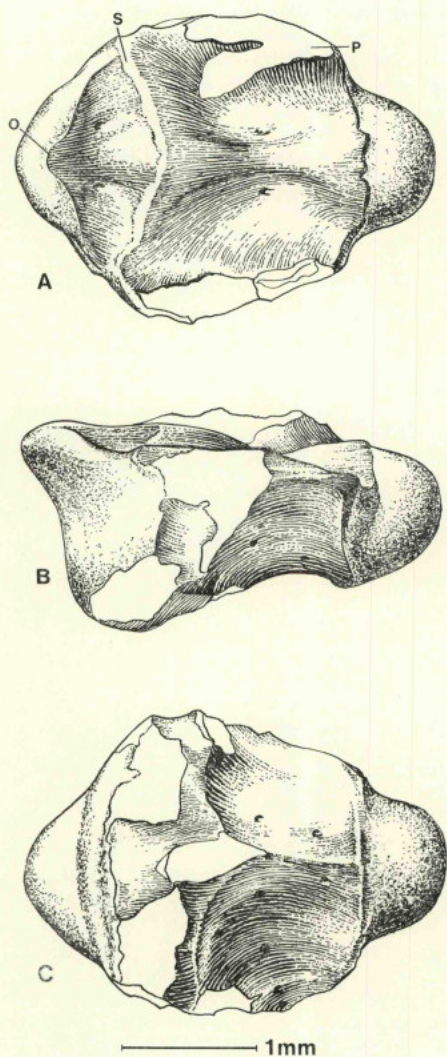
Fig. 47 — Epistropheus (Gui. L. 123); A: dorsal view, the neural arch has been broken off, the pleurocentrum of C_1 has been fused with that of C_2, O — odontoid process, P — pediculus arcus, S — sulcus intervertebralis; B: left lateral view, distinct odontoid process; C: ventral view, in the middle the regio intervertebralis.

The arch halves do not grow together dorsally as they are separated from the ventral hypocentrum on the base by a synchondral juncture. The wedge-shaped hypocentrum (Gui. L. 169) compounds the annular atlas ventrally. An anterior articulary facet is projected to the occiput to take in the medial condylar part of the basioccipital. The caudal articulary part bears the axial odontoid.

Right and left of a ventral apophysis (prominentis ventralis), each is located an opening for a vessel in the anterior part of the hypocentrum. As seen on a fragmentary hypocentrum, a third foramen can appear under the caudalarticulary area, and
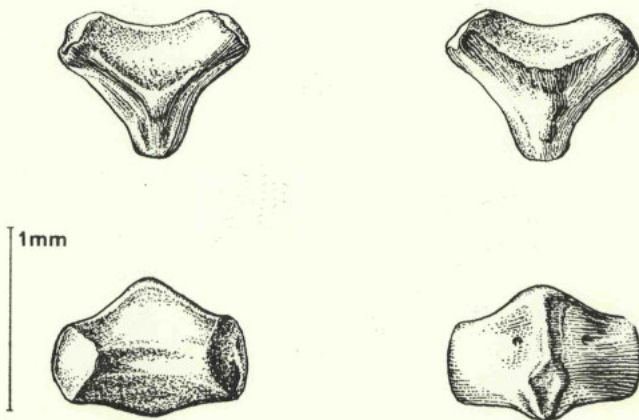
Fig. 46 — Atlantal hypocentrum (Gui. L. 169); above left: cranial view; above right: caudal view; below left: dorsal view; below right: ventral view.

is also useful in determining the facet. All five atlantal hypocentra have developed a prominentia ventralis. The atlantal articulary areas are lightly concave.

The large, cranially extended basidorsalia with postzygapophyses and the habitus of the hypocentrum are characteristic of scincomorph lizards.

In the Guimarota material the axis is represented by three specimens (Gui. L. 123) of the same type and two single odontoids. The pleurocentrum of the first cervical vertebra is fused with that of the second one; in part a weak suture is recognizable. The axis has a posterior condyle indicating the procoelian position of the following vertebrae. The second hypocentrum of the Sauria in general develops an anterior hypapophysis which is either fused with the centrum or separated by a suture and only affixed by tissues to the centrum. There is no indication of fixture point for the third intercentrum on the axial centrum, but by reason of the configuration of the ventral condylar area, a intervertebral position of the third intercentrum can be assumed, as this has also been deduced from the yielded post-axial vertebral fragments.

Both fused pleurocentra of the atlas and the axis present several foramina nutricia, which are bilaterally distributed by a cranially broadened median crest. The intravertebral compressing of the chorda is traced through the vertebral bone and reveals an hourglass-shaped relief on the dorsal side of the pleurocentrum of both atlas and axis and with bilaterally layered foramina nutricia. The neural arches of all the three specimens are broken. Below their base a synapophyseal process, which is directed
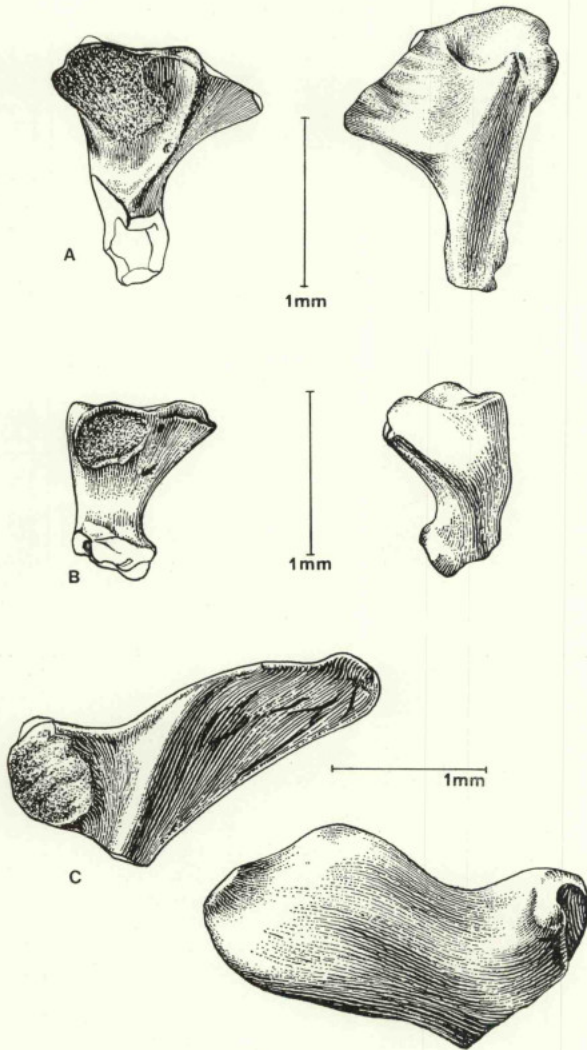
Fig. 45 — Upper parts of left halves of the atlantal arch from the Guimarota material (Gui. L. 168); A: left — medial view, postzygapophysis, right — lateral view, dorsal apophysis (diapophysis) and a diapophyseal groove; B: left — medial view, postzygapophysis, right — antero-lateral view; C: medial view and right — dorso-lateral view, dorsal apophysis.

The solid basal parts of the atlantal arch with its double-articulary facets are obviously suitable for fossification, whereas the fragile top parts and the ventral basal piece (hypo- resp. intercentrum) are often lost in the natural maceration or are broken, which I could equally well observe of *Lacerta lepida* and *Chalcides chalcides*.

The Guimarota mine yielded fourteen right (Gui. L. 165) and thirteen left (Gui. L. 131) basal parts, three right (Gui. L. 143) and four left (Gui. L. 168) dorsal parts of the atlantal arch and also five atlantal hypocentra (Gui. L. 169).

Only by the means of the four left dorsal arch fragments can three taxa be postulated. Two of these forms have distinct postzygapophyses, one specimen offers a neural arch which is anteriorly elongated in a medial direction, whereas the other can be distinguished by a relatively larger postzygapophysis and by a notch on the external side. In this way the posterior diapophysis is detached. The right arch fragments are certainly related to this described form.

The pedicels of the vertebral arches (Gui. L. 131 and Gui. L. 165) reveal that most of these fragments must have developed an arch top with a postzygapophysis. Therefore this type of atlas is numerous.

In comparison with some preparations of recent *Lacerta lepida, Chalcides chalcides* and *Varanus* sp., two foramina on the internal side of the arch next to the postzygapophysis are identified as the openings for blood-vessels.

As the second spinal nerve (N. cervicalis II) of lacertilians exits through the foramen intervertebrale between atlas and axis, the dorsal foramina in the diapophyseal groove are suited for the entry of blood-vessels. From comparative anatomy, it is known that the paired vertebral artery branches off rami spinales to the spinal cord, running between the long cervical muscles and the vertebrae. Beneath the spinal cord these accompany the Arteria spinalis anterior and the two lateral Arteriae spinales posteriores, all of which originate cranially in the A. vertebralis. As an important paired vessel, the occipito-vertebral artery runs from the aorta to the cervical vertebral column; on the atlas it bifurcates into an ascending arteria and a recurrent A. vertebralis dorsi, which runs along laterally the zygapophyses, and caudally units with the lumbal artery. This A. vertebralis dorsi gives nutritive rami for the dorsal cervical musculature and the spinal cord and anastomoses with the collaterals of the vertebal arteries. From these a vessel passes ahead of the postzygapophysis between the atlas and axis into the vertebral channel; there a connection can be suggested to the both described internal foramina. Externally a ramus branches off to the diapophyseal groove.

The Squamata generally have only one transverse process (synapophysis) on each side of the vertebra. The mode and position of the vertebral processes are embryonically induced by the arrangement of the muscles, the connective tissue and the ribs. This function conditions the differences in the location of the apophyses and also within the vertebral column. The external side of the basal fragments of the atlantal arch bears an apophysis, which is probably formed by the insertion of a trace of connective tissue like that in recent lizards. If an additional apophysis (diapophysis) is found to exist on the dorsal arch above the postzygapophysis, then this can be named parapophysis. The parapophyses are accompanied by foramina nutricia, usually by a larger posterior opening and a minute anterior one. However the latter is sometimes lacking.

The sides of the fragments are easily determined, considering that the posterior articulary facet of the basidorsale is only a little bigger than the anterior one, — the fact results from the articulation with the anteriorly tapered dens epistrophei. The atlanto-occipital articulation is smaller. Moreover both halves of the atlantal arch extend cranially.

1) **Regio cervicalis**

a)   Atlas and axis:

The two anterior cervical vertebrae have certain characteristics; the lacertilian atlas consists only of the neural arch and a ventral hypocentrum, which corresponds with the intercentra between the other vertebrae (centra). The true centrum of the atlas is constructed as a typical pleurocentrum, but co-ossifies with the second cervical vertebra (axis or epistropheus) and forms the anterior part of it, the odontoid.
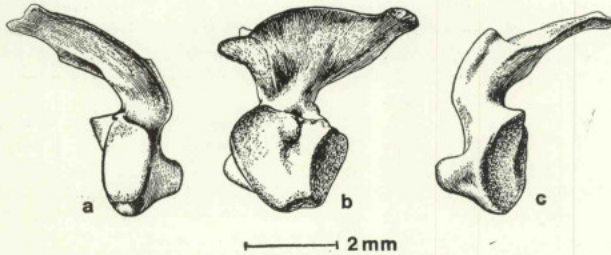

Fig. 43 — Left part of the atlantal arch of a recent *Lacerta lepida* DAUDIN, 1802; a: cranial view; b: medial view, left above the postzygapophysis; c: caudal view, left below the parapophysi.s

A complication in the construction results from the development of the cranial sclerotome half ahead of the atlas. This rudimentary vertebral design is termed proatlas. Whereas the hypochordal strap (hypocentrum) of the proatlas grows together with the occiput, parts of the neural arch are annexed to the atlas. The pleurocentrum of the proatlas becomes a small trunnion (processus odontoideus) on the odontoid (pleurocentrum of the atlas) of the axis.
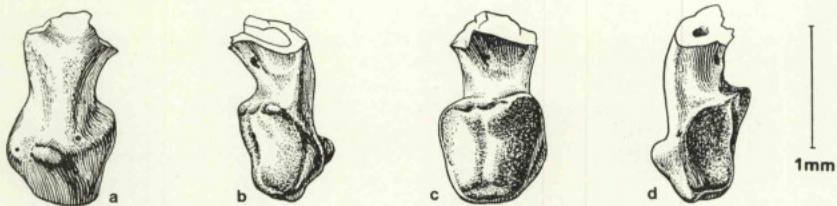
Fig. 44 — Basal part of the right part of the atlantal arch (Gui. L. 165); a: lateral view, parapophysis; b: caudal view, articulary face for the odontoid of the axis and the beginning of the postzygapophysis (above); c: medial view; d: cranial view, articulary face for the occipital condyle.

Both halves of the neural arch of the annular atlas generally remain disconnected from the ventral hypocentrum, nor do they unite above the neural channel. The articulary area for the occipital condyle is formed by the basal parts of the arches, the hypocentrum and in the middle, by the tip of the odontoid process. A septum interarticulare (ligamentum transversum) running transversally separates the processus odontoideus from the neural channel and two synergetic articulations, the atlanto-occipital and the atlanto-axial, from each other.
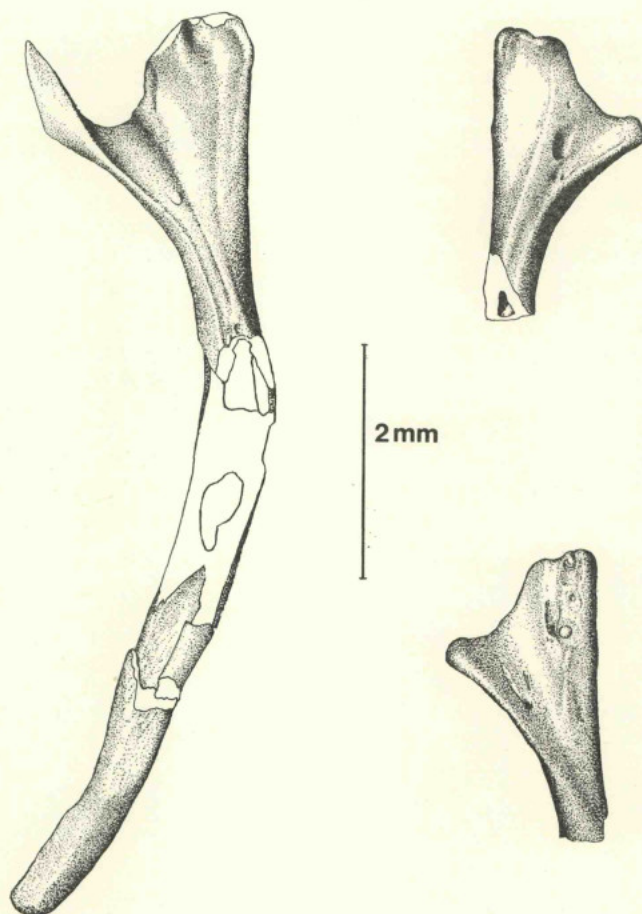
Fig. 42 — Pterygoids from the Guimarota material; left: Gui. L. 202, dorsal view
of a left pterygoid; right: Gui. L. 135, fragment of a right pterygoid (above:
dorsal view; below: ventral view, toothed processus palatinus).

perichordal vertebra is most important in the discrimination of the features in the
axial skeleton of the different vertebrate groups.

As a result of the presence of the lacertilian vertebral fragments, one can now
discuss the vertebral column under the following headings: cervical, trunk, pelvic and
tail region.

Fig. 41 — Gui. L. 149, supraoccipital; above: postero-dorsal view, anteriorly in the middle the processus ascendens; below: cerebral view.

Fig. 40 — Gui. L. 130 basioccipital; above: dorsal view, with fragmentary beginnings of the exoccipitals; below: atlanto-axial view, tripartite condylus occipitalis.

Gui. L. 35

5 mm

2 mm
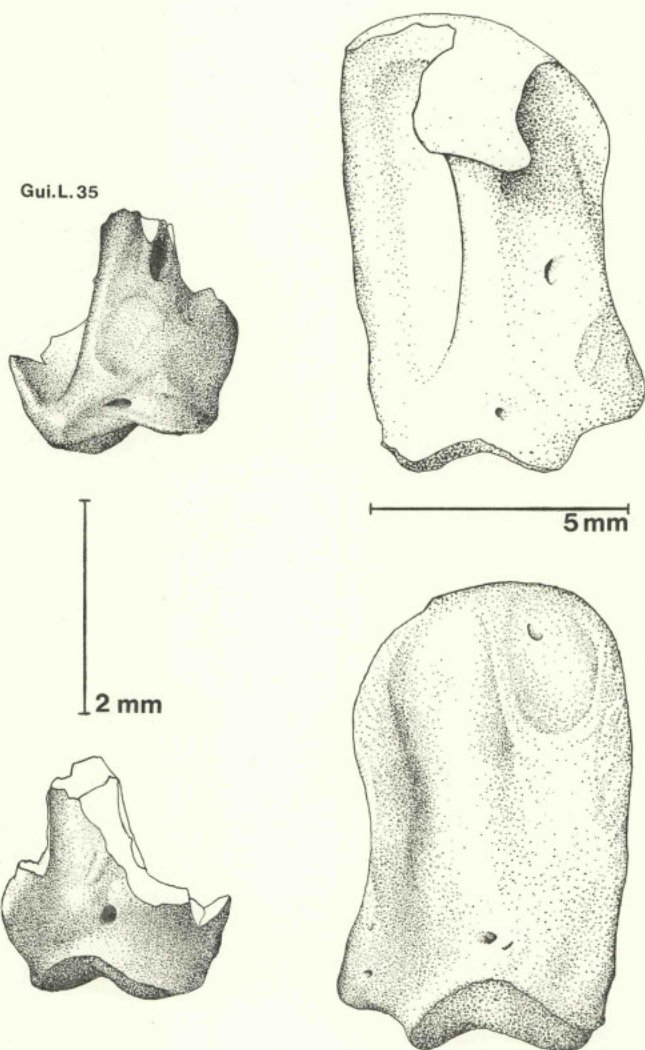
Fig. 39 — Gui. L. 35, fragment of a left quadrate from the Guimarota material in comparison with a left one of the recent *Lacerta lepida;* above: facies posterior; below: facies anterior.

5) **Ossa occipitalia**

The supraoccipital bone constitutes the occipital roof and also supports the parietal bone. From Guimarota a typical lacertilian supraoccipital is found (Gui. L. 149); on the dorsal side it offers a merial crest, which anteriorly continues into the processus ascendens supraoccipitalis. The configuration of the lateral processes indicates the connection with the posttemporal arch (i. e. with the processus paroticus of the exoccipital bone) and the presence of a transversal oval posttemporal opening.

The basioccipital bone Gui. L. 130 presents a tripartite occipital condyle and the fragmentary beginnings of the ascending exoccipitals on the upper sides. The piece Gui. L. 126, prepared with palavit, reveals a part of the capsula sphenoccipitalis. The occipital condyle of this specimen is not tripartite but small and hemispheric. The supraoccipital roof is broken by the intense deformation of the pieces. The processus paroticus (or paroccipitalis after EL-TOUBI, 1938) of the exoccipital bone seems to be extended laterally in a straight line. A sphenoid process of the basioccipital is preserved. The anatomical features of the presented occipital bones are best compared with those of the Scincidae.

6) **Os pterygoideum**

In the Guimarota material the pterygoid is represented by more than 50 fragments, which, if they have been preserved, are toothed. The pterygoids seem to extend backwards considerably (s. Gui. L. 89 and Gui. L. 202). When the jaws are in occlusion, level with the coronoid, a process of the pterygoid branches off for the connec-
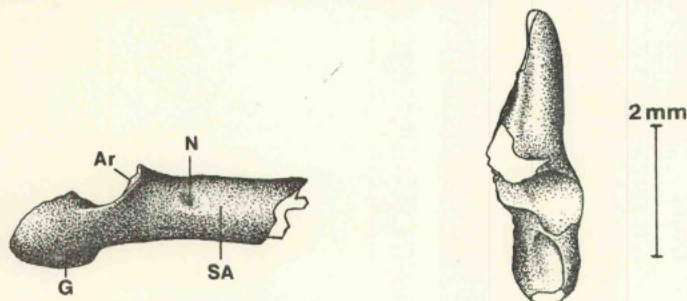
Fig. 38 — Gui. L. 2, posterior end of a right lower jaw; left: lateral view, Ar — Articular, G — Gonial (=Pre-articular), N — For. nervi auriculo-temporalis (N. V₃), SA — Surangular; right: dorsal view, articulary area for the quadrate.

tion with the ectopterygoid (or os transversum after HAAS, 1936 and VERSLUYS, 1936). At this junction point of the pterygoid with the processus ectopterygoidalis and the processus palatinus with mince teeth, there are some differences in the shape, the thickness, the broadness and the quantity of the pterygoid teeth. These features imply the existence of at least four taxa.

G. The vertebral column

From the history of development, we know that the axial skeleton of the vertebrates consists of two components derived from different germinal cells: the entodermal Chorda dorsalis and the mesodermal perichordal skeleton. The genesis of the

and on the anguid *Diploglossus;* but these lacertilians reveal another run of the groove. There are some frontalia fragments (Gui. L. 237) with a smooth surface and a long, small, incurved lateral ridge, too.

3) Os jugale

The jugal is represented by 30 angled specimens, which present, without exception, the entire characteristic reduction of the inferior temporal arch. The piece Gui. 193 (a left jugal fragment) indicates a mince process directed to the quadrate; it documents the primary quadrato-jugal junction of the ancestral lepidosaurs. The same is to be seen in a lower degree on the jugals Gui. L. 125, Gui. 143, Gui. L. 239.

The processus maxillaris, which is directed forwards, is differently developed; on the specimen Gui. L. 125 it shortly becomes thin to the maxilla, whereas on Gui. 143 and Gui. L. 239, it is rather more long than broad. The external side of the processus maxillaris jugalis presents a linear row of several foramina on most of the jugals; the specimens Gui. 107 and Gui. 193 do not have them.

By the prominent orbital margin on the internal side, a sulcus is developed in the angle of the jugal but not so on the specimen Gui. 193. The different jugalia forms certainly suggest that five lacertilian taxa exist.

4) Squamosal, quadrate and articular

Regarding their angled shape, the squamosals Gui. 94, Gui. 149 and Gui. L. 240 could be mistaken for the jugals, but in contrast to the jugal, the squamosal bones have a short posterior, rounded end forming the articulation with the quadrate and an anterior one with a medial attachment area for the postorbital.
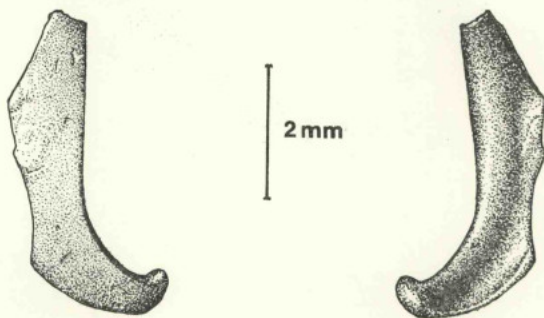
Fig. 37 — Gui. 94, right squamosal, showing the shape of a hockey stick [cf. ROBINSON, 1967b].

The numerous quadrate fragments indicate the free motility (streptostyl of these bones. The basal ends are developed for a saddle-articulation with the articular of the dentary. The mobile junction to the pterygoid is marked (s. Gui. 53).

46 articulation pieces of the articular are presented; on several of them the channel for the auriculo-temporal nerve (N. V.$_3$) is to be seen running from the external side into the fossa Meckeli. The processus retro-articularis does not bend downwards (s. Gui. L. 2).
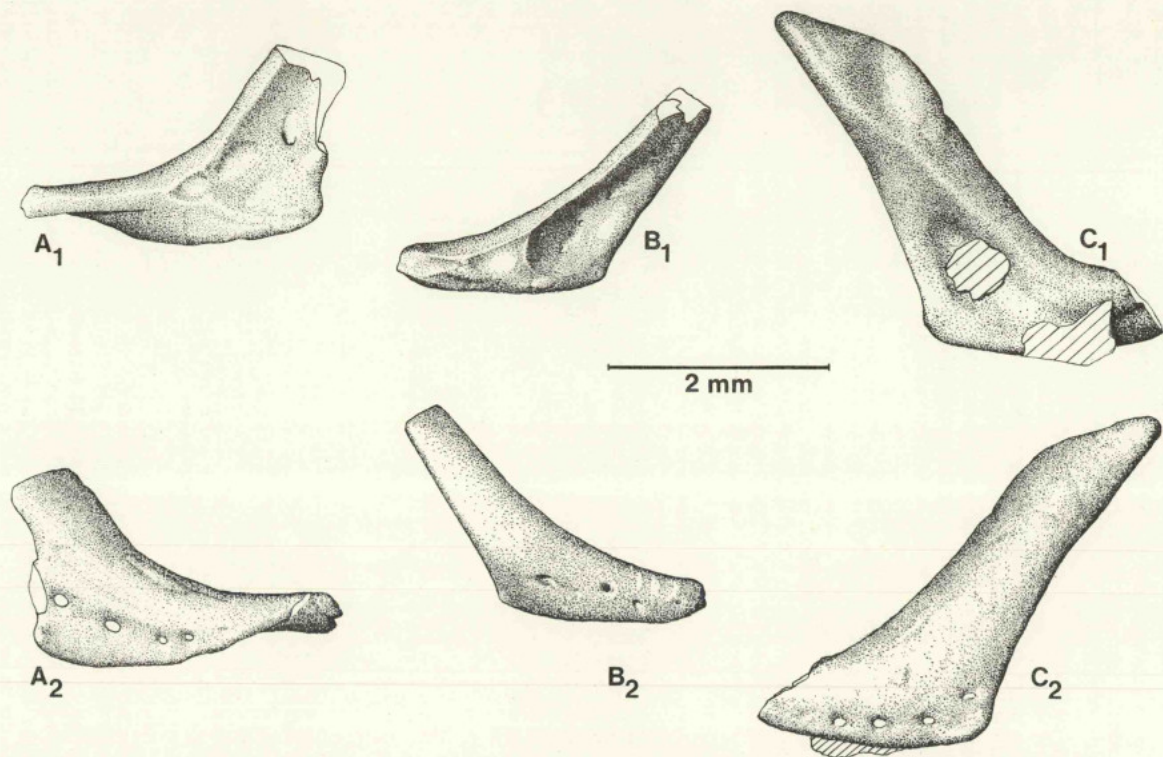
Fig. 36 — Different lacertilian jugals from the Guimarota material; A: Gui. L. 125, right jugal with a relatively short maxillary process; B: Gui. L. 239, right jugal; C: Gui. 143, left jugal; 1: medial view; 2: lateral view.
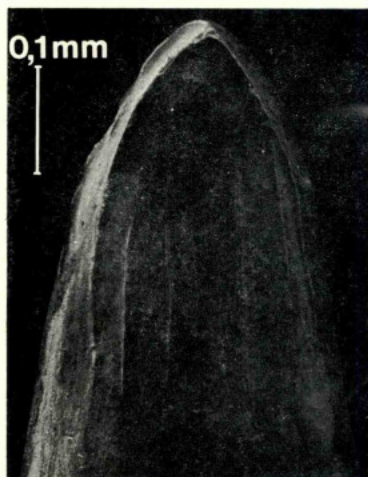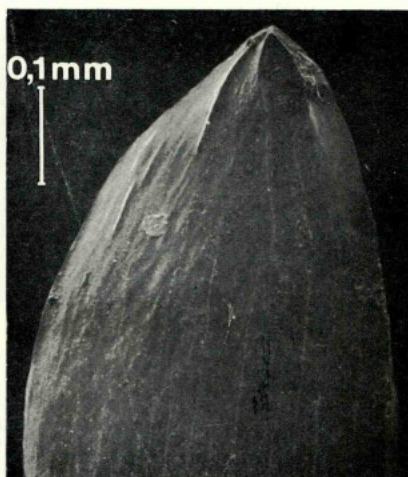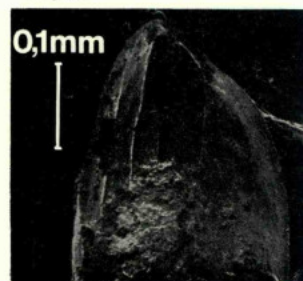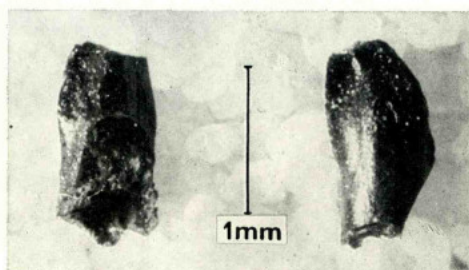
Fig. 1

0,5 mm

Fig. 2

0,1mm

Fig. 3

0,1mm

Fig. 4
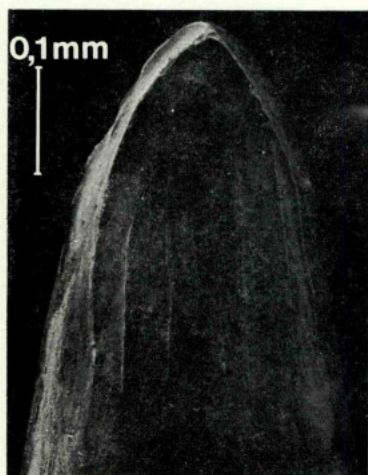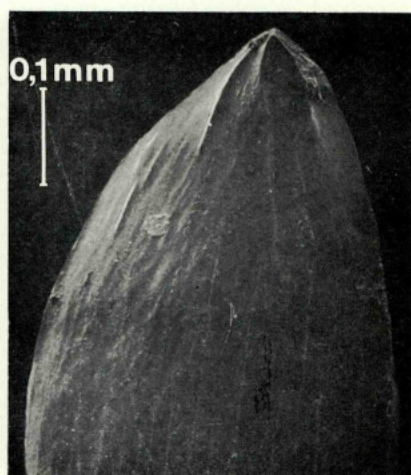

0,1mm

Fig. 5

1mm
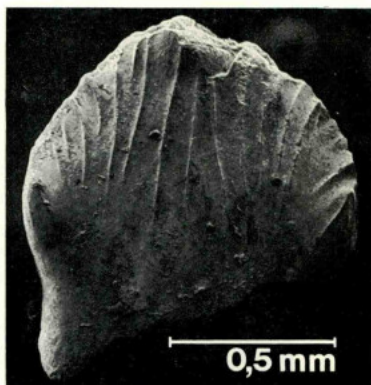
Fig. 6

Fig. 1

Fig. 2

Fig. 3

Fig. 4
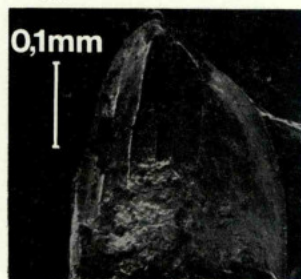
Fig. 5
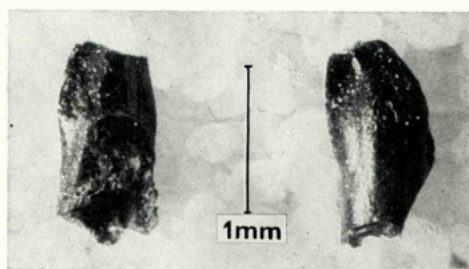
Fig. 6

PLATE II

Fig. 1 — Gui. L. 34, right maxilla of *Becklesisaurus hoffstetteri*, labial view, with osteodermal relief.
Fig. 2 — Gui. L. 31, right maxilla of *Becklesisaurus hoffstetteri,* labial view, smooth surface with foramina maxillo-facialia.
Fig. 3 — Gui. A. 56, *Becklesisaurus hoffstetteri*, left dentary (holotype), lingual view.
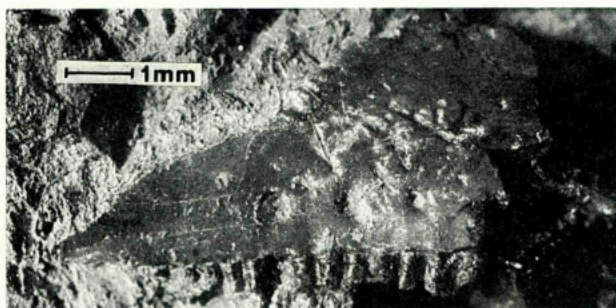
Fig. 1
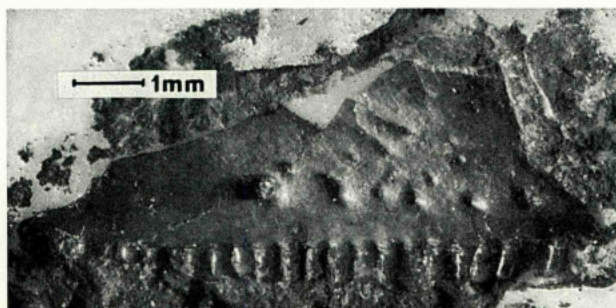
Fig. 2

Fig. 3

PLATE III

Fig. 1 — Gui. 5, *Saurillus* cf. *obtusus* OWEN, 1855, lingual view of a right dentary with a narrow Meckelian groove.

Fig. 2 — Gui. 7, *Saurillus proraformis*, right dentary (holotype), lingual view, posteriorly broad Meckelian groove.

Fig. 3 — Gui. 6, *Saurillus henkeli*, left dentary with splenial and processus dentalis of the coronoid (holotype), the subdental ridge remarkably thins out to the splenial and coronoid.
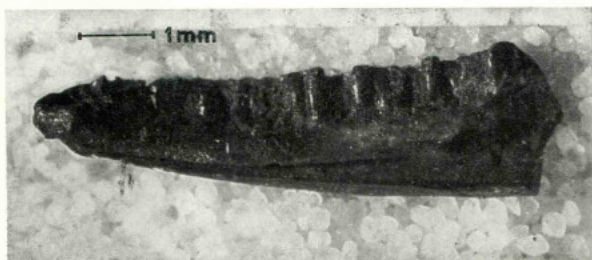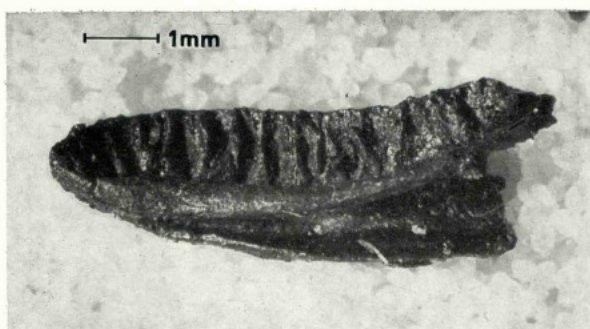
Fig. 1

Fig. 2

Fig. 3

PLATE IV

Fig. 1 — Gui. L. 4, proximal part of a right ulna, left: facies lateralis, right: facies radialis.

Fig. 2 — Gui. L. 85, right pelvic girdle, visceral view; the pars pubica reveals a relatively large foramen obturatorium.

Fig. 3 — Gui. L. 221, distal part of an ulna; left: facies lateralis, right: facies radialis.

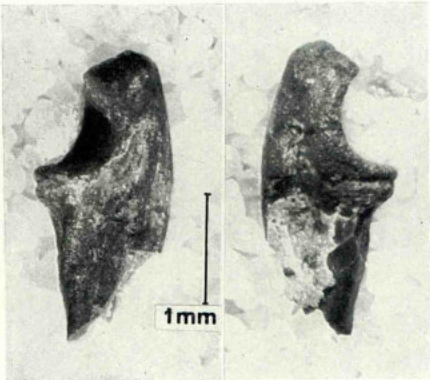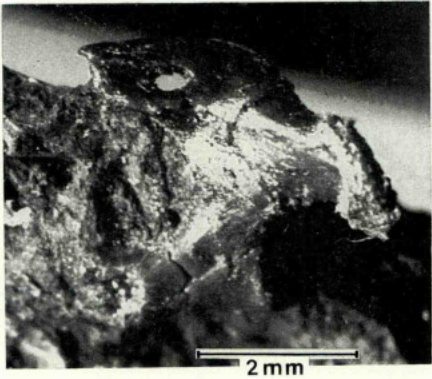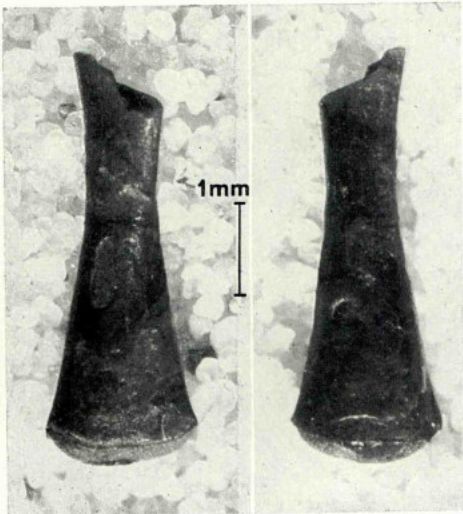Fig. 4 — Gui. L. 171, distal parts of two right radii with processus styloideus.
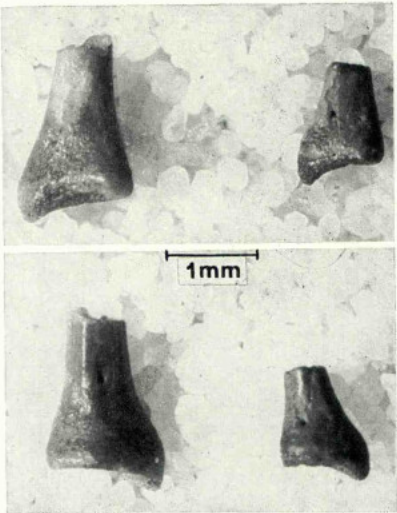
Fig. 1

Fig. 2

Fig. 3

Fig. 4